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A QUANTITATIVE STUDY OF THE MIGRATION OF THE PAINTED LADY BUTTERFLY, *VANESSA CARDUI* L.

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INTRODUCTION

The painted lady butterfly, *Vanessa cardui* L., also called *Pyrameis* or *Cynthia*, is almost worldwide in distribution, and its migrations in Europe and North Africa have been known for centuries. Williams, in his "Migration of Butterflies" (1930), devotes an entire chapter to the records he has accumulated on the migration of this species. Yet these reports are inadequate in that each is based almost wholly on observations made at a single station during a few days at the peak of a migratory period. Little exact attention has been given to the extent of any migration in space or time. The reports from North America are particularly incomplete.

Since his first contact with a migration of this species in 1924, the present author has been impressed with the lack of exact knowledge of the subject. This paper attempts to distinguish between fact and impression, to put our knowledge of the subject on as quantitative a basis as is possible to date.

The type of migration is classified on the basis of William's discussion as a unidirectional flight with no return. To the author this seems a better term than emigration, which emphasizes only point of origin, or than immigration, which emphasizes only destination. Inasmuch as there is lack of knowledge of both origin and destination, the present paper will use the word migration freely with no efforts at exact delimitation. Also, in the interests of simplification, the word "butterfly" will refer to this species only, unless otherwise stated.

A migration is recognized when the butterflies, whether few or many, are all at the same time flying in the same direction, as if guided by a compass. Whether they are maintaining an even altitude a few feet above the ground, or dipping up and down after the manner of a goldfinch, or flying high over obstacles, they maintain a straight flight, so far as ordinary observation can detect.

At the height of a migration, the butterflies are noticed in flight by many observers for a few days, or in an exceptional migration, like that of 1924, by the general public; but a careful observer, in a migration year, finds that the migration period extends nearly two months, sometimes even longer. In either case, there is one point of almost unanimous agreement: the direction of migration over southern California is in general toward the northwest, north-northwest, or north. An exception is news, and sure to be recorded.

All of the material here discussed refers to the spring migration, as there is no evidence of a return fall migration in North America. Two instances of a north or northwest migration in late summer, probably of a second generation, have been recorded. Lotrich, as quoted

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by Woodbury *et al.* (1942), observed a flight in Monarch Pass, Colorado, in a northerly direction, on August 20, 1935. W. Hovanitz, in a letter to the author, dated September 18, 1944, records from memory a north or northwest migration in Pasadena, California in September–October, 1940, which, incidentally, had not been a migration year.

History of This Study

The present year, 1949, marks the fifth migration in southern California in a quarter of a century. Migrations have occurred in February–March, 1924; February–March, 1926; March–April, 1941; March–April, 1945; and March–April, 1949. Reports have been made to the San Jacinto Section, Western Society of Naturalists, 1926; the Western Section, Ecological Society of America (Abbott 1941, 1946, 1949); and a summary of the twenty-five year period was given to the Seventh Pacific Science Congress, Auckland, New Zealand, February, 1949 (Abbott 1950).

The central point at which the observations were made is Redlands, San Bernardino County, California (figs. 1, 2). Redlands is at the east end of San Bernardino Valley, at the west end of San Gorgonio Pass, which is the connecting natural highway from the Colorado Desert. It is also in direct line, twenty miles across the east end of San Bernardino Valley, with El Cajon Pass, the connecting natural highway to the Mojave Desert and northward. It thus appears to be on an important migration route for birds, and offers an opportunity to investigate whether butterflies follow a natural migration route.

Parallel studies have been reported from Utah (Woodbury *et al.* 1942; Sugden *et al.* 1947), mentioning flights in 1924, 1930, 1931, 1935, and describing more extensively migrations in 1941 and 1945. This shows only a partial coincidence of flight years between Utah and California. It is also interesting that, in 1941 and 1945 at least, the flight in Utah averaged a month later than in California, and was in general northeastward. The absence of migrants from many miles of intervening Colorado Deserts suggests, although it does not prove, a different source of the migrants.

Acknowledgments

This study has been possible because of the cooperation of a large number of observers, named or unnamed, whose aid is hereby acknowledged. Special mention should be made of Elizabeth Nichols Abbott, who worked directly with the author in field observations; Roy Cain, who made daily records while travelling over San Bernardino County during the entire season of the 1945 migration; Robert C. Dickson, who made daily counts at one station in 1926; and Margaret Salmond, whose observations of the daily cycle in 1941 filled in a number of gaps in the picture. Aside from those acknowledged in the text, data included in this paper were contributed by N. Abbott, F. E. Adams, J. Adriance, L. M. Ashley, B. Balcom, B. Bartolomea, M. L. Behlow, J. W. Bell, P. Bell, R. Beswick, F. H. Billings, G. J. Blum, L. Boheim, N. M. Brown, B. Burchfield, E. Butler, M. Colvin, D. Cox, J. Decker, A. Dowden, P. Fiesell, F. Foote, B. Ford, G. George, G. Gibbs, M. F. Gilliam, E. Gird, H. Goldberg, Y. Goya, W. Haddock, B. Hammerschmidt, L. Hand, R. Harriman, M. Hart, R. D. Harwood, E. Henry, R. L. Hickcox, H. M. Hill, M. P. Hodges, W. Jackson, M. James, A. Kelsey, F. Kresse, M. Long, V. Mackie, C. Malby, M. Margetts, V. K. Mayo, J. E. McBride, L. E. McVay, L. M. Mihel, M. H. Miller, E. Newman, E. G. Norton, P. Null, E. Perkins, O. D. Pfeiffer, M. Reamer, R. G. Redding, P. Rittenhouse, K. Ritter, R. Rolens, F. Rugg, T. Schmidtmann, F. A. Sihler, A. Sparkuhl, D. Stafford, B. L. Talbot, J. T. Tavis, L. Taylor, W. B. Townsend, E. Trottier, R. Weaver, T. L. Winkler.

Figures 1 to 4 inclusive were drawn by William W. Clarke, Jr.

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Methods

The methods of obtaining data, varying somewhat between the years, may be summarized as follows:

1. Daily counts to determine comparative rate of migration. These were made regularly at Redlands by R. C. Dickson and the author in 1926, and are supple-

mented by volunteer counts in 1941 and 1945, both at Redlands and at widely scattered localities.

2. Intensive analysis of the migrating behavior by the author and his students, chiefly on the University of Redlands campus, in 1941 and 1945.

3. 1941 reports of dates and duration of migration over southern California from responses to a postcard questionnaire; also from students at their homes or travelling during their spring vacation.

4. 1945 reports from over southern California in response to a request through the daily press for information.

Geographical Extent of the Migration

The recorded extent of the migrations of 1941 and 1945, determined by correspondence with volunteer observers, is given in figure 1. In order to make the map helpful and not confusing, only such place names are given as are needed in

Fig. 1. Southern California, showing area in which migration was studied in 1941 and 1945. Place names indicate localities where migration was observed which are referred to in the text. Arrows indicate points from which direction of flight was reported. Highways shown are chiefly those followed by observers.

reading the text. Arrows indicate reported direction of flight. Highways shown are those travelled by observers during the migration.

The area covered extends from the California-Mexico border north nearly to Inyokern and Shoshone in the northern part of the Mojave Desert. Over this entire region, roughly 225 miles from south to north and 225 miles wide at its greatest extent, butterflies were migrating for nearly two months, with rare exceptions in a north or northwest direction.

During this period, migration appeared to be simultaneous over the entire area. Large numbers were observed on certain groups of successive days (waves of migration), followed by smaller numbers, with a probable relation to weather conditions, discussed later. It is not possible in the reports to detect a gradual change in numbers from south to north, indicating a progressive movement of the entire body of migrants. It must be remembered, however, that aside from the records at Redlands and San Bernardino, practically all of the reports were of single days or successive days of unusual abundance, i.e., peaks of migration only. Little was contributed as to the beginning or ending of the migratory period or of a gradual increase in numbers in any other locality. The migration at Redlands will be discussed under "seasonal distribution."

A word is in order as to the reasons for making a combined map for the two years 1941 and 1945. The reports from the belt extending westward from Redlands and San Bernardino to Los Angeles indicated comparable conditions and numbers in the two years. In the rest of the area, the 1941 reports, made in response to requests for information at selected localities, gave the better picture of the early part of the flight, from the Mexican border northward. The 1945 reports, in response to requests for information through the San Bernardino Sun and the Los Angeles Times, covered better the Mojave Desert area (mostly in San Bernardino County), and the country directly north of Los Angeles. Together the reports for the two years cover most of southern California and give a more complete picture than either year taken separately. There are enough southern reports in 1945 and northern reports in 1941 to warrant the belief that the extent of the migration in the two years was much the same.

A cross section shows simultaneous migration from the coast eastward to the middle of the deserts on the highways as far as Shoshone, Needles, and Desert Center. There appears to be a thinning out as the shore of the Pacific is approached, while the drier parts of the deserts form a distinct eastern boundary. It should be noted, however, that the migrating butterflies are not evenly distributed over the area. This can be observed by travelling across a migrating path. Large numbers may be passed through, followed by regions where the butterflies are quite absent. W. S. Wright reported one such instance in 1926 when he passed through three distinct migrating paths in one afternoon in driving 60 miles east from San Diego.

A definite analysis of such a migratory path was made by the author at Redlands from March 16 to 22, 1941. During those days the center of the migration was approximately through Redlands with thinning out to an east boundary at the entrance to Mill Creek Canyon and a west boundary at Pigeon Pass on the Riverside road (fig. 2). This gave a path of migration about 14 miles broad. Then on March 22 to 23 the center seemed to shift toward the west, with large numbers reported from the Colton-Riverside area.

Another observation of a distinct boundary on a single day was made by the author on March 1, 1924. Accompanied by S. S. Berry and Clyde Searl, he attempted to follow the migrants from Redlands through San Bernardino to Cajon Pass. The butterflies were all flying in a northwest direction west of the

pass, and not a single migrant was found in the pass.

According to reports collected by Williams (1930, pp. 202, 203), the larger 1924 and 1926 migrations continued north through both the coastal counties and the interior valley. Smith and Linsley (1945) reported a migration in progress in Contra Costa County, northern California, in late April, 1945; but no reports were received from the intervening San Joaquin Valley to establish connection with the migrants of the Mojave Desert.

Scattered reports in 1949 tell of a migration in San Diego, April 1–11 (J. Ballin); in Newhall, April 3 (R. E. Galbreath); and in the San Bernardino area, April 6–13 (R. Cain). The author observed a steady migration at Redlands April 8 and 12, but only isolated individuals west of Loma Linda. He also observed thirteen single migrants in Santa Monica and West Los Angeles on scattered days from March 8 to March 30, suggesting the extreme western boundary of the migration area. Due to temporary absence from Redlands, an organized study was not made this year.

Until 1949 no exact information was available as to breeding areas in northern Mexico. On April 3, 1949 a breeding area in Baja California was discovered by J. S. Garth and E. Y. Dawson of the Hancock Foundation, University of Southern California. It was located on a promontory on the shore of Santa Maria Bay, which is about 600 miles SSE from San Diego, and is classified by Grinnell as Lower Sonoran Life Zone.

As described by Dr. Garth (private communication), thousands of butterflies were observed, many of them emerging

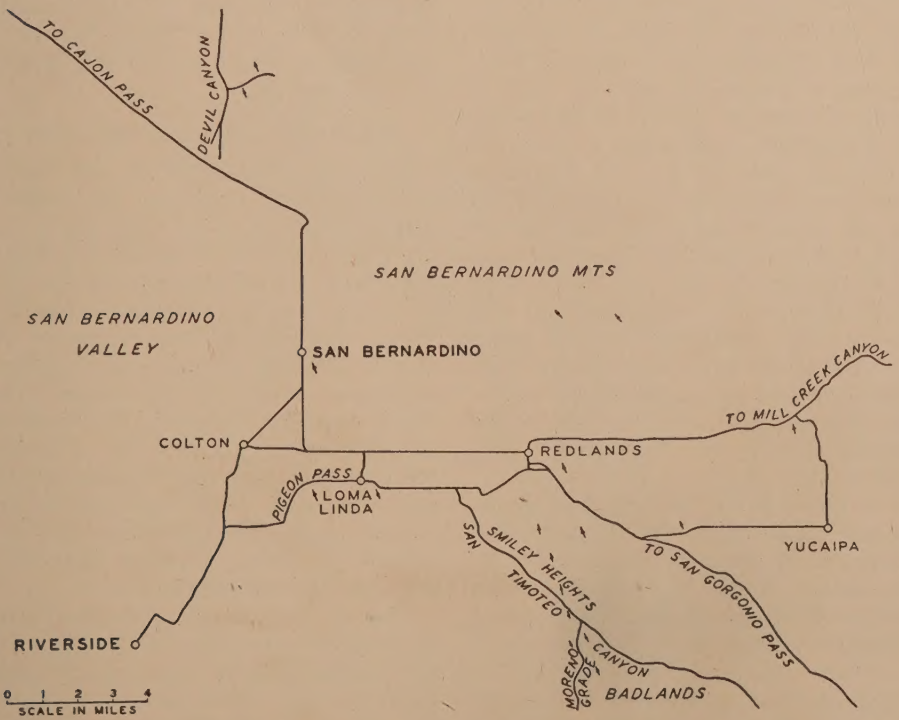

FIG. 2. Redlands-San Bernardino region. Arrows indicate observations of flight direction in 1941. Highways are those followed in making the observations. This map shows a northwest migratory path which disregards topographic features.

from the chrysalid state. There was no indication of a northward migration. Many butterflies flew south a short distance to the edge of the cliff, then north again to the breeding area.

The following day, April 4, a few were observed around the ship on San Hipolito Bay, 200 miles farther north. There was an offshore wind from the Viscaino Desert.

While there is as yet no proof that these individuals of *V. cardui* were destined to migrate north into California, it is significant that they were observed in a migration year, and at approximately the same dates as in California. If these are points of origin of the California butterflies, they add greatly to the probable distance of flight.

Relation of Flight to Topographic Features

Figure 2 is an enlarged map of the region directly around Redlands illustrating that the direction of flight is independent of topographic features. This is important, because there is an idea popular among bird students that a northward migration route follows San Gorgonio Pass, or its adjoining San Timoteo Canyon, to the east end of the San Bernardino Valley, crosses the valley, and continues northward through Cajon Pass which zigzags first west, then east. It may be added that while these two passes are used to-day by transcontinental railroads and highways, they do not represent the earliest trails into the valley (Beattie and Beattie 1939, pp. 3, 19), used by the Indians.

On figure 2 may be traced an actual typical course taken by the butterflies (indicated by arrows). As observed by the author, March 19, 1941, butterflies were not flying directly down San Timoteo Canyon, although that direction would have been in general northwest. Rather they came over the hill labelled Badlands, descended at an angle into the branch canyon labelled Moreno Grade, crossed this canyon, rose over the hills, then descended and crossed San Timoteo Canyon, rose at an angle over Smiley Heights at the southwest border of the city of Redlands, and continued across the city.

Moreno Grade descends through a branch canyon with fairly steep walls. One would suppose that a butterfly following a definite direction as if controlled by a compass would fly across the top of the canyon from rim to rim. Actually the butterflies followed down the east wall and up the west wall, keeping about the same distance from the ground all the time. The same observation was reported by students from the steeper walls of Devil Canyon, north of San Bernardino, during the same week.

As to Cajon Pass, observations have shown almost everything except butterflies flying directly up the pass. When observed in the pass, they have regularly been flying northwest or west, usually across the pass. It has already been mentioned that on March 1, 1924, they missed the pass entirely.

Relation to Vegetation Types

The vegetation types of the region where the flight originates, the territory through which the flight takes place, and the area reached before cessation of flight, are shown diagrammatically on the Life Zone map of southern California (fig. 3). The Lower Sonoran Zone represents the deserts, and also the hot, interior valleys which are favorable for citrus fruits. The Upper Sonoran represents the brush or chaparral which covers much of southern California foothill and coastal region, and is in some places cultivated to deciduous fruits. The Transition Zone represents the lower forested mountains, dominated by the yellow pine.

Popular theories and somewhat scant evidence give the origin of the flight under Lower Sonoran conditions, although the possibility of its being also under Upper Sonoran conditions has not been eliminated. It continues northwestward through both indiscriminately, crosses the

mountains through the Transition Zone, if not higher, and continues into the Lower Sonoran conditions of the Mojave Desert. This does not appear to be a change from one vegetation type to another.

A closely related question, related to current population theories, is concerned with variation in the abundance of larval food in a region where the vegetation is dependent on an irregular, scant rainfall. It is accepted, that this species lays its eggs on food plants suitable for the larvae, and that a considerable range of food plants may be used (Comstock 1927; Essig 1926; Holland 1900). Abundance of food plants may, therefore, be considered under the heading of abundance of vegetation in general. In certain years in the deserts, and to some extent in the chaparral, there is a notable abundance of wildflowers, which means abundance of larval food. Is there any relation between a wildflower year and an increase in population resulting in a migration year?

A difficulty in the application of this theory is the fact that while migration

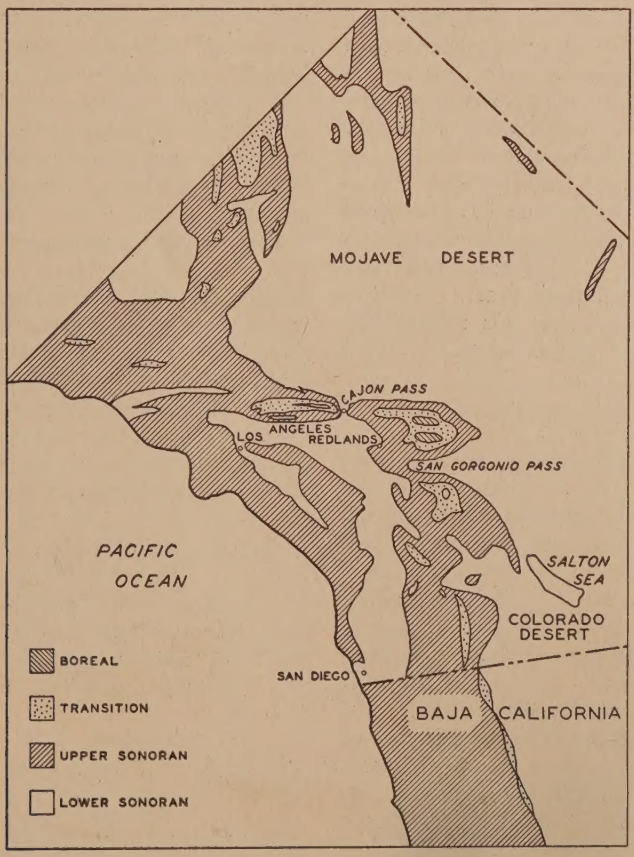

FIG. 3. Life zones of southern California. Comparison with figure 1 shows that flight northwest was through both Lower Sonoran and Upper Sonoran conditions, with many of the butterflies crossing the Transition Zone of the mountains and ending the flight in the Lower Sonoran Mojave Desert. (Redrawn from map in Wyman and Burnell, 1925, by permission of Houghton Mifflin Co.)

years are definitely recognized, there seems to be no accurate way to define a wildflower year. Not finding published records of the occurrence of such years, I have consulted Norman C. Cooper, Carl Epling, Ethel Higgins, E. C. Jaeger, Harlan Lewis, and F. W. Went as to their memory of wildflower years. Since the term is not exactly definable, and since the adundance of wildflowers is not uniform among the varying environmental conditions of desert and chaparral, the information obtained is not entirely consistent. Briefly, wildflowers were abundant in 1924, 1941, and 1949, but not in 1926 and 1945. They were also abundant in 1935, in which there was a butterfly migration in Utah, but not in California. There appear to have been some years of wildflower abundance which were not migration years, but exact information is not available. Summarizing, some migrations have occurred in years of abundant vegetation, but none are recorded as occurring in the year next following a wildflower year. The importance of considering this relationship is discussed later in this paper.

Direction of Flight

One of the most striking characteristics of a migration of this butterfly is the steady, consistent flight in a constant direction. Not only does this apply to all the butterflies flying in one locality on a particular day, but there is a prevailing direction over the entire area of migration included in this study. It is conveniently described as northwest although it varies from west-northwest to north-northwest or north. The same is true of the wind, which is often spoken of locally as a north wind, although it almost always blows from west of north. Most observers used the same symbols, whether NW or NNW or N for both direction of flight and direction of wind; that is, the butterflies were flying against the wind according to the accuracy of ordinary observation. In this paper this direction of both flight and wind is usually designated as NW.

The result of this constancy of direction is that only a departure from it becomes an event to be recorded. It is natural to neglect to record it when there is no variation. This is important in compiling the statistics, because otherwise the exceptions would be overemphasized. Failure to record the direction of flight and wind is usually in practice equivalent to a NW record of both flight and wind, a conclusion based on personal experience, contact with a large number of observers, and a knowledge of the consistent nature of the migration and the wind direction. (Compare table V, presented below in connection with another topic.)

The common impression that flight is normally directly against the wind is not, however, supported by the statistical material available as strongly as would be expected.

Table I gives a summary of the direction of flight in relation to direction of wind in the 1945 reports, the only year in which most of the reports included wind direction. In the list where direction of flight and wind were both recorded, only 18 out of 27, or 66⅔% are flight against the wind. Out of the total list, the largest number which could possibly be construed as flight against the wind is 40,

Table I. *Direction of flight in relation to direction of wind, 1945*

Angle between flight and wind	No. of records
Complete records:	
0° (against wind)	15
45° (against wind)	3
90°	3
112.5°	1
180° (with wind)	2
Uncertain	3
Total	27
Incomplete records:	
* Direction of flight given	19
* Direction of wind given	3
Apparent difference between flight and wind	2
No wind	1
Relation uncertain	2
Total	27

* Presumably flight was against wind.

74% of the total. The number of exceptions, at least one-fourth, is large enough to show that the direction of wind cannot be the only factor determining the direction of flight, even if it is an important one.

The most striking observations on a direct relation between flight and wind were made on the afternoon of March 28, when the following observations were confirmed independently by several observers placed at various stations on the University of Redlands campus.

1. The wind was SSW, but somewhat variable.

2. Some groups of butterflies were flying in the usual NW direction, while some were flying SSW against the wind.

3. Butterflies which approached the lee side of a hill, flying NW, changed their course when they came to the top of the hill, turning and flying against the SSW wind. While they were turning, one single butterfly was seen to keep on toward the northwest.

4. It was reported from Banning (twenty miles east) on the same afternoon that the butterflies were flying directly against a SSW wind, and the same report came the next day from Beaumont (fifteen miles east).

These records of March 28, 1945 indicate a direction of flight precisely determined and changed by direction of wind, but they are an isolated example.

The following are our only reports of flight in the same direction as the wind. It is noteworthy that they are very few, not in exact relation, and details are missing in most of the reports. Only three of them are in 1945.

Mar. 16, 1941. Cajon Pass. Flying down pass, SE direction, late afternoon, wind strong (W. Malone).

Mar. 29, 1941. Santa Ana Wash, north of Redlands, middle of afternoon. Flying W, wind SE (C. H. Abbott).

Apr. 5, 1941. Burbank and Pasadena. Flying SW, wind E (reported independently by A. Ellerman and A. Swift).

Mar. 26, 1945. San Bernardino. Flying N, wind S (slight) (R. Cain).

Mar. 29, 1945. Redlands. Flying NW all afternoon. At 5 P.M., when they were still flying NW, an ENE wind had developed (H. Richard).

Mar. 30, 1945. Hermosa Beach. Apparently had been flying NW, but turned E when a strong W wind developed (J. Ballin).

Letter of Apr. 26, 1926 from W. S. Wright, San Diego. Flights W always preceded by E wind from desert.

The total number of records here given on relation of wind and direction of flight may not seem large (54), although it compares well with the 51 records which Williams (1930) compiled from all sources to show the same points. The results differ from those of Williams in that he records an equal number of flights with and against the wind, whereas in California we have only a negligible number of instances of flight with the wind.

It is not possible to conclude from these figures that the wind is the major controlling factor. It is also difficult to eliminate it as a factor. The records of SSW flights on days of SSW winds cannot be ignored, as this takes the butterflies out of the prevailing direction of migration.

There is no observed gradation in the effect of varying strengths of wind. The flight is evenly against the wind whether the wind is strong, medium, or weak, and apparently the same where the wind is imperceptible to a human observer. In one or two instances quoted above, it is possible that the insects were blown by a strong wind, but, as compared with almost daily observation of flight against the wind, these instances do not seem important.

Height above Ground

The height of flight above the ground shows a considerable degree of individual variation. It is also true that, when passing over a level field, some butterflies appear to fly an even distance above the ground, while others, perhaps fewer, dip up and down. It is also noticeable that they regularly fly over obstacles, even

tall eucalyptus trees, rather than go around them.

To test whether all of the butterflies kept close to the substratum, the author watched them from the roof of the three-story Hall of Science at the University of Redlands. The observer found himself looking down on all the migrants except those passing over trees. It was noted that the latter flew high enough just to clear the treetops, and immediately descended if there were no other obstacles in the way.

When the butterflies, flying from the southeast, came against the south wall of the Hall of Science, two types of behavior were noted. Many of them stopped to feed at a large lantana bush on the south wall, and, on leaving, flew west along the wall until beyond the building, when they

TABLE II. *Height of flight above ground (observations of M. Salmond, March 18, 1941)*

Number	Height above ground
8	4 feet
7	3 feet
1	2½ feet
6	2 feet
Average	3 + feet

turned northwest. On the other hand, some of them, particularly those which did not contact the lantana, on reaching the wall rose in the air in a spiral and passed over the roof, continuing northwest. This behavior was watched both from the ground and from the roof, and was very characteristic.

Estimates of the height above the ground by various observers varied from 1 to 15 feet, but by far the largest number reported 2 to 4 feet. To show that this is only an average, consult table II. This average, approximately three feet above the ground, agrees with most of the estimates of other observers.

RATE OF FLIGHT

The rate of flight has previously been reported to average slightly over nine miles per hour (Abbott 1950). This, however, is only an average. Each individual appears to have its own rate of flight.

TABLE III. *Time of individual butterflies in flying 100 feet over level ground (observations with stop watch by A. Ellerman and R. Harrington, March 18, 1941)*

Number	Time per 100 feet (seconds)
1	14.0
1	10.0
1	9.0
1	8.5
4	8.0
1	7.5
5	7.0
1	6.5
1	6.25
2	6.0
1	5.5
1	5.0
Average	7.562 sec. = 9.02 m.p.h.

As an example of individual variations, table III records the time taken in flying 100 feet over level ground.

RELATION OF FLIGHT TO WEATHER AND CLIMATE

Hours of Flight

The general observation is that the hours of flight are the hours of brightest sunshine, and that foggy mornings, common in southern California in spring, delay the beginning of the daily flight. It also appears that cloudy days show fewer migrants, and that during a period of cloudy and rainy weather the migration is interrupted.

TABLE IV. *Hours of flight during day (observations at Redlands, California, by M. Salmond)*

1941	Flight began	Flight ended	Weather
March 18	10:20 A.M.	4:50 P.M.	Fair
March 19	12:15 P.M.	3:30 P.M.	Cloudy
March 20	9:00 A.M.	3:20 P.M.	Fair
March 21	8:20 A.M.	4:40 P.M.	Fair
March 22	9:00 A.M.	4:20 P.M.	Fair
March 23	8:40 A.M.	4:15 P.M.	Fair
March 24	8:40 A.M.	4:30 P.M.	Fair
March 25	8:20 A.M.	4:25 P.M.	Fair
March 26	8:15 A.M.	5:15 P.M.	Fair
March 27	8:35 A.M.	4:10 P.M.	Fair

Migration practically ceased in the rainy week between March 29 and April 4.

Table IV, covering ten consecutive days of a migration, gives a definite picture of the hours of flight, and is typical.

It is interesting to calculate the time it would take an individual butterfly to cover the 225 miles of the migratory area here described. This can be done, although nothing is known as to whether an individual butterfly covers the entire distance; and the figures do not make allowances for stopping to rest and feed or for bad weather.

In table IV, for the eight days of fair weather, March 20–27, the average number of hours of flight per day is 7.75 hours. From table III the average rate of flight is approximately 9 miles per hour. This makes 69.75 or close to 70 miles as the possible distance a butterfly could travel in one day if it flew continuously. To go 225 miles would therefore take a little over three days.

Redlands data, given in the next section on seasonal distribution, show that the steady flight recorded in table IV had been developed gradually from a beginning at least as far back as March 9. Comparing these figures with those just given on mileage per day shows how a flight which had been going on for three or four days could be recorded on the same day throughout the entire area, as most observers note the butterflies only when they become abundant.

Seasonal distribution; waves of migration

Table V is based on daily five-minute counts during the noon hour made by R. C. Dickson throughout most of the 1926 migration, excluding week-ends. It is here included because the counts are comparative, and the direction of flight and weather conditions are stated in each case.

It will be noted that the direction of flight varied only between west-northwest and north-northwest except on Feb. 16, 18, and Mar. 8, all days of very small flights. The periods of greatest flight (peaks of migration), Feb. 17, Feb. 22–24, Mar. 11 were all fair weather, which was probably true of Mar. 17, 18. In contrast, very few migrants were reported on the cloudy days, Feb. 15, 16, Mar. 4–8, and none on the rainy days Feb. 12–14, Mar. 7, 9, 19.

TABLE V. *Butterflies passing between two points (Hall of Science and Administration Building, University of Redlands, width of 100 feet) on days named in direction indicated (data of R. C. Dickson)*

1926	Weather	Direction of flight	Number in 5 min.	Number flying in reverse direction
Feb. 11	F(air)	NW	53	2
Feb. 12,13,14	R(ain)		No migration	
Feb. 15	Cl(oudy)	NW	5	4
Feb. 16	Cl	E	2	1
Feb. 17	F	WNW	425	
Feb. 18	F	W	21	2
Feb. 19	F	NW	34	
Feb. 20,21			Heavy migration	
Feb. 22	F	NW	160	
Feb. 23	F	WNW	204	
Feb. 24	F	NW	312	
Feb. 25	F	NW	32	3
Feb. 26	F	NW	53	2
March 1	Lt.Cl.	NW	6	1
March 2	F	NW	64	3
March 3	Lt.Cl.	NW	55	2
March 4	Cl.	NNW	9	
March 5	Cl.	NNW	22	
March 7	Sh(owers)			
March 8	Sh.Cl	N	5	1
March 9	Cl,Sh		0	
March 10	F	NW	46	1
March 11	F	WNW	500	
March 12	F	WNW	70	7
March 15	Broken high Cl	WNW	45	1
March 16	F	NW	73	
March 17	Broken Lt. Cl	NW	121	2
March 18	Breaking Cl	NNW	127	
March 19	R			

The following five-minute counts by the author on days of extensive migration may be compared with those in table V.

Feb. 5. Average of 66, based on 5 counts at different stations.

Feb. 6. Average of 57, based on 4 counts at different hours.

Feb. 17. A peak day. Later counts at 6 different stations averaged 242.5.

Feb. 25. The day following a peak day, diminishing counts showed 102 at 8:20 A.M., 35 at 9:15 A.M., 40 at 10:10 A.M., 5 at 2:45 P.M.

Mar. 11. A peak day. 220 at 11 A.M., 62 at 5 P.M.

During this same period, the author's daily observations and many counts showed such a close correspondence with Dickson's figures that he has combined the results in figure 4, using Dickson's

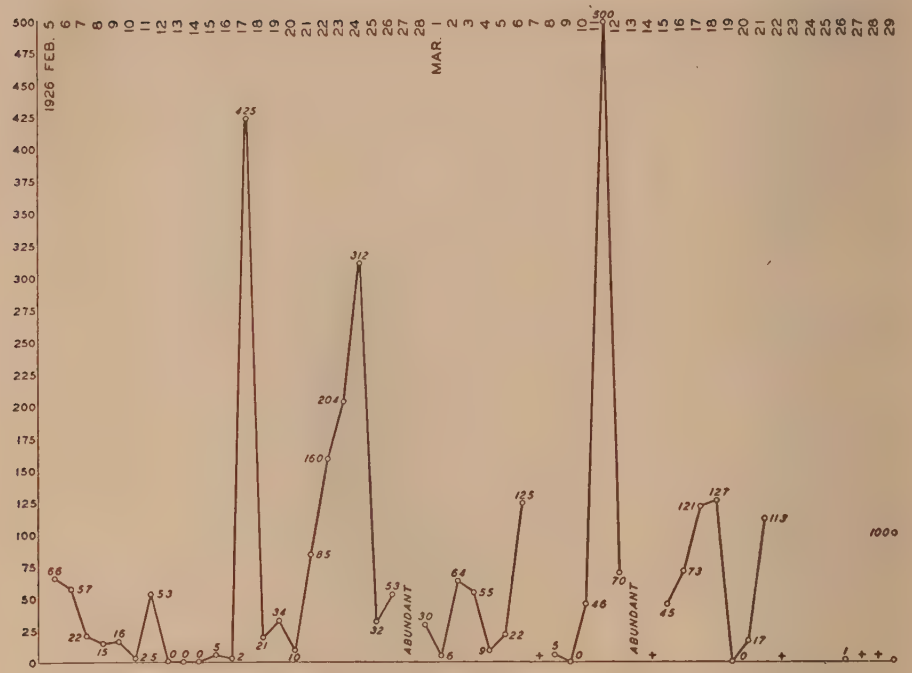

FIG. 4. Daily record of numbers of migrating butterflies throughout the 1926 season, based on 5 minute counts (see text). Waves of migration are shown. Data of R. C. Dickson and C. H. Abbott.

figures when available, and his own on the missing days. The chart traces the migration from February 5 to March 29, and shows peak flights on Feb. 17 and 24 and Mar. 11; and lesser peaks on Feb. 5, 11, and Mar. 2, 6, 18–19, 21, and 29.

As to agreement with reports from other localities, Miss F. G. Conrad reported a peak flight in Los Angeles Feb. 23. W. S. Wright reported them numerous in San Diego Feb. 20–26, and another peak flight Mar. 11–13, with its height Mar. 11, the same day as at Redlands.

In 1941 comparable daily counts were not made, but, from single counts and exact descriptions furnished by a large number of observers, it was clear that the first wave began Mar. 9, increased to a maximum at Redlands Mar. 21 and west of Redlands, Mar. 22–23, decreasing to Mar. 28. Following a week of cloudy and rainy weather, a second wave began Apr. 4, reached a maximum Apr. 6, and ended Apr. 7. The third wave was from Apr. 15–22, with the largest counts on Apr. 17.

In 1945, with reports from a still wider area, periods of abundance were reported Mar. 19–21, Mar. 24–25, Mar. 27–29 but continuing to Apr. 4, also Apr. 7 and Apr. 15. The dates coincided from the coast to the edge of the Mojave Desert, and also in the Mojave Desert so far as reports were received.

Relation of flight to local climatic conditions

An examination of the maps shown in figures 1 and 3 shows that any summary of climatic conditions must take into account an apparent origin of the flight in either desert or chaparral conditions or both. The changes in environmental conditions during flight are greater for butterflies originating in the

desert than for those from chaparral, yet except as indicated, the following statements will hold for both.

It should be borne in mind that the initial stimulus for direction of flight is determined at the place of origin of the flight. There is little if any evidence that flight into a different set of environmental conditions changes the direction. It is, however, possible that such a change in environmental conditions is one of the factors responsible for a gradual discontinuance of the flight.

(*a*) *Temperature.* The flight is toward a cooler temperature, whether toward the coast or in a general northwest direction. The only apparent exception is that many of the butterflies cross the mountains and spread out over the Mojave Desert. But it is to be remembered that the low altitude Colorado Desert, where part, at least, of the flight seems to originate, is very warm in March and April, while the high altitude Mojave Desert is slow in warming up in spring and usually considered cool at this season. A cool wind might be the determining factor in the initial flight.

(*b*) *Moisture.* The situation with regard to atmospheric humidity is much less clear. The initial flight is in general toward more moist conditions, as the northwest winds carry moisture from the ocean over the region southeast of Los Angeles. But farther east, in the San Bernardino Valley, which was the central point of the study, strong drying winds blow directly from the Mojave Desert. Flight from the San Bernardino Valley into the Mojave Desert is flight toward a drier atmosphere. It must be remembered that this could be one of the reasons for the discontinuance of the flight.

(*c*) *Wind.* The fact that the flight is most commonly against the wind and the butterflies are not blown by the wind has already been discussed. The relation of wind to temperature and moisture has already been considered under (*a*) and (*b*).

(*d*) *Rain.* Migration ceases during rain, and is much reduced on days of heavy clouds. This may be the chief explanation of the waves of migration. On this hypothesis, a steady migration during a period of pleasant weather constitutes a wave, while a period of cold or rainy weather interrupts it.

(*e*) *Sunlight.* The flight begins in the morning at about the time the sun strikes the insect, and the usual direction of flight is somewhat away from the direction of the sun at that time in the morning. If the sun is a factor in determining the direction of flight, it is not the only factor, because the same direction is kept up all day in spite of the gradual shifting of the direction of the sun. The possibility has been mentioned, however, that the initial stimulus may determine the direction of the entire day's flight.

In the absence of direct experiments on the combined influence of these environmental stimuli on *V. cardui,* a few notes on other animals will suggest possibilities for work.

Shelford (1913) introduced a method for the study of the reaction of the smaller land animals to gradients of moisture and temperature. Chapman (1931), in a study of sand dune insects, applied the principle to the specialized field of desert animals, showing a more exact reactivity in the animals which are less protected structurally against evaporation. Kendeigh (1934), applying the principle to birds, concluded that sensitivity to temperature is the most important factor in causing bird migration, more so than length of day. For birds this conclusion is important, because it accords with observations of east-west migrations in California which a length of day theory cannot explain (Grinnell 1908); and also with the Life Zone theory, which Grinnell (1935) shows to be so distinctly applicable to bird distribution in California.

A further illustration of the influence of moisture, temperature, and light on animal behavior, and the difficulty of separating them is found in the shore isopod, *Ligyda occidentalis.* As observed by the

author at La Jolla, these isopods collected during the day in crevices between boards on a westward facing sea wall. In the deep twilight of early evening the isopods came out, and spread widely over the wall and the beach. Whether it was a negative reaction to light, a positive reaction to the pronounced increased moisture on the beach, or to lower temperature, was difficult to determine. Daytime observations indicated that these factors acted independently in varying degrees, and that in the main moisture was the key factor, as at times it completely overshadowed the others (Abbott 1940).

A tentative hypothesis is that the butterflies fly from a warmer to a cooler region, from a drier to a moister region, and that when they get into optimum conditions they keep on in the same direction so long as the conditions remain the same. The constant wind might be a factor in maintaining the optimum conditions. The optimum condition could be a balance between temperature and moisture, rather than the dominant influence of one of them, a relationship which is extensively analyzed by Chapman (1931).

Discussion

The migration of *V. cardui* is a spectacular instance of mass migration of animals which is not described as a plague, because the larvae are rarely destructive of cultivated crops.

The observations here described are based entirely on field work, and, so far as is known to the author, have never been compared with laboratory experiments. With a hope that this may be done at some time in the future, the present knowledge is summarized as follows:

The following features of the migration are consistent:

1. The same territory is covered in every migration, the extent varying with the total numbers.

2. The season of migration is constant, southern California spring, February and March or March and April. The time duration is also fairly constant, averaging slightly under two months.

3. The direction of flight is constant, northwest, varying toward west or north, with other directions only occasional.

4. The direction of flight is usually against the wind, which, whether or not the wind is causal, results in a constant relationship to the wind and to other environmental factors which wind might modify.

5. The territory reached as a result of the migration is no more favorable for larval food, and therefore for breeding, than is the territory from which the migration comes. The indications are that the flight ends gradually, a partial list of possible causes being fatigue, or stopping to breed, or a drier atmosphere.

The most important questions to which this study attempts to contribute are:

1. The reason for migration, including the irregular intervals between migration years. Under this head comes also the daily stimulus for continuing the flight and the interruption due to unfavorable weather.

2. The factors controlling the direction of migration. This includes consideration of wind direction and the influence of wind on temperature and moisture changes.

The general principle, that a mass migratory movement is often the result of a sudden increase of population, has been so well known over so long a period of time that it is difficult to give priority to any formulation of the principle. There is also considerable evidence that in some species (notably the lemmings of north Europe), the migrations occur at regular intervals, although in more instances, such as locusts, crickets, and mice in North America, the occurrence is irregular and unpredictable.

Under the head of reason for migration are two questions: What is the reason for the increase in population? Why does increase in population result in migration?

Chapman (1939) gives an excellent analysis of how an increase in population may be due to a lowering of environmental resistance. He also relates this to the potential rate of increase of the species (biotic potential). The higher the biotic potential the more rapid is the effect of lowered environmental resistance. The lowered resistance may be at any critical period of the life history. Schrader (1928) reared *V. cardui* in captivity, and obtained 685 caterpillars from a single female, which is a high biotic potential for an insect.

In the section on vegetation types, one possible method of lowering environmental resistance was discussed, namely, an unusual amount of spring vegetation on the desert. With a species as prolific as this, a single favorable season might result in a tremendous temporary increase in population. The relation might be something like this: usual abundance of larval food in the early spring would result in the development of unusually large numbers of larvae to maturity, provided an excess of eggs had been deposited by the preceding generation. Or, the influence of unusual rainfall might act directly on the insect, activating more eggs or inducing better larval development.

As was said in the section referred to, conclusions on this point await more evidence of a correlation between insect abundance and vegetation growth.

Chapman (1939) mentions migration as one of the well known results of a sudden increase in population, but does not follow up the point with any discussion of the reasons. If migration occurs in a year of abundant food, as the preceding discussion suggests, it could not in those years be due to a scarcity of food plants on which to lay eggs. There is some evidence that migration may be due to the overcrowding of adults. As to how the latter might work in the case of insects and particularly butterflies, Heape (1931, pp. 161-170) outlines a theory of the way in which the intense activity of butterflies hatching out in unusual numbers in a limited area might result in what may be described as first play, then hysteria, and finally mass emigration in the direction taken by the leaders, whatever factor may have been the cause for that initial direction. Heape continues: "So the flight goes on continuously, unbrokenly, at first in smaller, then in much greater numbers, which gradually dwindle till made up only of stragglers, the last to gain their freedom, who, however, struggle valiantly after the main body. Such flights are always described as undeviating and regardless of obstacles. They do not seem to be intelligently or instinctively directed toward some favorable breeding area."

Referring again to the behavior of *V. cardui* in Baja California, described by J. S. Garth, the activity which preceded migration, provided these same individuals were to migrate, is very similar to the theoretical description by Heape. It shows that overcrowding may involve other factors than competition for food supply.

The migration having started, the the daily stimulus due to sunshine and the interruptions due to cloudy and more particularly rainy weather seem to be well established, as far as the data of the present study show. These, however are annual, affect non-migrants as well as migrants, and while they appear to be supporting factors, they do not seem to be adequate causal factors of migration.

The other subject, the control of the direction of migration, was discussed under the headings of wind, temperature, moisture, and sunlight. The initial daily direction, usually toward the northwest, is away from the sun and toward the daytime wind, which in most of the country studied, brings air that is somewhat cooler and more moist. Apparently only a radical change in any of these factors later in the day will change the direction of flight. So few instances of such a change have been observed that no evidence has been accumulated as to the

cause. This direction of flight is favorable to the insect so far as physical factors are involved, but nothing indicates that such a change in environment is necessary to the insect.

It has often been noted that the abundance and widespread distribution of the butterflies in a migration year does not result in an increased population in the following year, either at the point of origin, along the line of flight, or at the destination. If eggs laid by these migrants hatch a little later in the season (Woodbury *et al.* 1942), the larvae face a long, dry season with little chance for many of them to develop. Any eggs remaining dormant until the next spring would be dependent on the combination of vegetation and physical conditions, which would rarely in two successive years be exactly right for the development of an excessively large generation.

Summary

Analysis of the migration of the painted lady butterfly, *Vanessa cardui* L., in southern California in the five most recent migration years, 1924, 1926, 1941, 1945, and 1949 has established the following points, as far as possible on a quantitative basis.

1. The territory covered in 1941 and 1945 was carefully mapped, and included most of southern California west of Salton Sea and north through the Mojave Desert. The area mapped is about 225 miles long and 225 broad at its greatest extent. In 1924 and 1926, when larger numbers were involved, the flight was followed north through the coastal counties and through the interior valley. A breeding area in Baja California, located by a Hancock Foundation expedition in 1949, may be an important point of origin.

2. The area of origin is certainly desert and may also include chaparral; the destination appears also to include both desert and chaparral. Other vegetation types are passed over indiscriminately. The path of migration is plainly not related to vegetation types, and the evidence of a relation to abundance or scarcity of food is conflicting.

3. The migration is distinctly in a straight line, usually in a general northwest direction, without regard to topographic features, such as mountains and canyons. Butterflies usually rise over obstacles, rather than going around them.

4. The flight is most commonly against the wind, but the large percentage of exceptions makes it doubtful that the wind is a decisive factor. Flight against the wind may bring the butterfly into a more favorable combination of temperature and moisture conditions, but the insects fly toward desert winds as well as toward moist winds from the ocean.

5. A migratory period extends over a long season, approaching two months, sometimes longer. It consists of a series of waves with a few distinct peaks. A peak flight appears to be simultaneous over much of the territory and to occur under favorable weather conditions. Sunny, warm weather is favorable; cloudy, rainy weather may interrupt the flight for several days. Flight is during the sunny hours of the day.

6. The rate of flight averages about nine miles per hour, and the estimated height above the ground averages about three feet. Both of these figures are averages, with considerable individual variation.

7. While all of these points which consistently recur suggest ways in which the environment partially controls this migration, they do not show any reasons why this species should migrate while other related species, apparently exposed to the same stimuli, do not. The pressure of population as a cause of mass migratory movements is still the only adequate theory proposed, and the observations here recorded are at least consistent with this theory.

8. Further studies needed are a detailed study of the life history of this species in southern California with emphasis on seasons of all stages of development, number of broods, and larval food plants. Laboratory experiments are

needed on the influence of dominant environmental stimuli, particularly moisture, temperature, light, and various combinations of these.

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DESCRIPTION AND RECORDING OF VEGETATION UPON A STRUCTURAL BASIS [1]

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The living environment of any organism may be approached in many ways: the divergences in point of view, method, technique and conclusions reflect the differences in purpose. The geographer, the ecologist, the taxonomist, the pathologist, the geneticist and others, many others, are interested in encompassing in a classification the living beings on which they work or which presumably bear some relation to a particular organism on which they are working. Some scientists are called upon to contribute to the edification or modification of systems of classification of the environment. But for the most part, they will have to adopt a ready-made framework since their principal objective lies elsewhere. They will also (at least formally) accept the implications which are usually read into the system itself and which lie at the origin of its elaboration.

My purpose is to review some of the most significant of these schemes and to bring out the ends for which I assume each one to be adequate. I have no intention of claiming greatest merit for any one system—even less for the one I am about to propose myself—as I believe that they can all be used with profit. I would only emphasize the scope of each one and point to the futility of applications exceeding it.

I have been attracted to this problem in the course of my association with geographers, many of whom I realized were in something of a predicament when their study called for an incidental but sometimes rather important description of the natural vegetation. A recourse to the essentially taxonomic or floristic work of the plant geographers De Candolle (1855), Drude (1890), Flahaut (*in* Coste 1901), Gaussen (1933), Wulff (1943), Cain (1944), Good (1947) seemed inadequate in actual descriptions of landscape. On the other hand, the detailed monographs of the phytosociologists (v.g. Braun-Blanquet 1936, Etter 1947), when available, contained too much irrelevant material and too much which was of difficult interpretation. The physiognomic systems (especially Schimper 1903, Warming 1909, Schimper and von Faber 1935) were decidedly at once more manageable and more germane to their purposes. Many, however, were desirous of incorporating a more dynamic point of view and referred to the concepts and vocabulary of Braun-Blanquet (1932) or Weaver and Clements (1938). For instance Taylor (1947) describing the biogeography of Canada, used Halliday's (1937) vegetation map as a background, but also included a purely floristic key to the species of pines!

Plant geographers and ecologists have provided some conclusions and classifications that geographers can use to a certain extent. They can hardly be expected, however, to have designed instruments for the geographer to work with, to use in the field and the laboratory, and for measuring already-collected data. This has been done recently (1947, 1949) by a geographer, Küchler, whose work is reviewed below.

The plight of the geographer is also that of many other scientists, with entirely different aims, when they come to a definition or description of environment. I hope to illustrate these various inade-

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quacies in the course of a brief review and a comparison of systems which follows. In so doing, I would point out the true and sometimes exclusive orientation of some of the concepts involved and the kind of relationship which they can be expected to underline.

The new system which I shall propose hereafter is primarily an attempt to free specialists in fields other than plant taxonomy and ecology from identifications of species and to provide them with a means of showing a certain number of environmental relationships and peculiarities, especially for purposes of comparison. It is also designed for the ecologist to use as a practical recording device and will be especially useful for the study of variation in structure of communities.

This system was first set up early in 1947, and has been revised and readjusted many times since then. A preliminary abstract was published in 1948. A more extensive exposé was presented at the Pacific Science Congress, Christchurch, New Zealand, in 1949 and will be published in the Proceedings of the Seventh Pacific Science Congress. The following colleagues, botanists, ecologists and geographers, have read various drafts of this paper: N. W. Radforth, N. A. Burges, S. A. Cain, D. B. Lawrence, J. W. Coulter, and A. W. Küchler. For their many valuable criticisms and suggestions I am most grateful. I am especially indebted to Dr. A. W. Küchler for his patient discussion and evaluation of the present system and for his excellent advice and to Dr. and Mrs. M. F. Buell for their careful criticism of the final manuscript. I owe much to Dr. F. E. Egler who pointed out many unclear statements and helped me restrict some of my broader assumptions. I wish to thank Miss Françoise McNichols who so ably undertook the task of drawing the illustrations for this paper from my rough sketches.

The many points which will come up in the following pages will force a passing reference to almost all important ecological principles. These cannot be dealt with or justified in most cases, although there is lack of general agreement on quite a few of them. I hope that I may not unduly stress my own "faith" in such matters and I have made an attempt not to use the language of a "school" exclusively although I am generally in sympathy with the Zürich and Montpellier approach to ecological problems (as outlined by Braun-Blanquet 1932). I must, therefore, apologize for numerous footnotes which will serve to indicate the place of long digressions and uncertainties. On some points I have attempted to elaborate my ideas more fully elsewhere (Dansereau 1945, 1946, 1951a, and in two unpublished manuscripts).[3]

The Floristic Point of View

The plant geographers cited above were essentially preoccupied with the distribution of individual species and the relative coincidence in geographic range of members of the same *flora*. Former positions and migrations, evidence of speciation and isolation and explanations of the mechanisms involved were thus brought to light. The criteria used by these authors, especially by Cain (1944), following the important contributions of the cytogeneticists or biosystematists (Dobzhansky 1941, Mayr 1942), when applied for instance to cultivated plants (Vavilov 1940, Mangelsdorf and Reeves 1939, Anderson 1946), have yielded results of the highest significance to the geographer.

In studies on speciation, where attention is focused on a particular group of organisms, the floristic boundaries (*e.g.*, in terms of Gaussen (1933) or Good's (1947) areas) are highly significant. In fact, they probably indicate the zones of large-scale fluctuation through great periods of time and it is not surprising that they do not coincide even with major plant formations as they happen to be

[3] (a) "An ecological classification of the species of vascular plants," and (b) "L'efficacité du climat et les inhibitions édaphiques."

distributed at this particular time. And yet, even for the purpose of etching in the environmental background to evolutionary processes, the floristic categories only afford a first approximation.[4] They are much too broad to encompass the concrete processes of variation and evolution which can be analyzed only on a larger-scale basis (see Stebbins 1950).

Floristic and geobotanical relationships are of no great help in the definition or description of the landscape, in that phase of physical geography where the texture of the biological background is investigated. For example, a knowledge of the geographical affinities of the endemics in the Gaspé Peninsula flora (Fernald 1925, Marie-Victorin 1929, Wynne-Edwards 1937, Hultén 1937), gives only an historical clue to present-day conditions. What is wanted at this stage is a description of the vegetation itself.

Many naturalists today (botanists, zoologists and ecologists) appreciate the predicament of both biologists (physiologists, geneticists, pathologists, anatomists, paleontologists, etc.) and geographers when confronted with the necessity of an accurate reference to the background of the organism or phenomenon they are about to study. In this respect, a failure to distinguish between flora and vegetation has caused a great deal of confusion. Egler (1942, 1947) has admirably reviewed and evaluated this situation. He has pointed to the many invalid interpretations which stem from faulty concepts and unclear ideas. Cain (1947) has also emphasized the respective limits of both approaches.

The flora of a locality or a region is the residue of all the plant species which, in the course of geological time, have occupied that territory and have successfully withstood the subsequent climatic and other vicissitudes or have taken refuge elsewhere and more or less recently reinvaded. As far as can be known, some of these indigenous species are autochtonous, others are derived from immigrant stocks favoured by diverse geological or climatic events. Recent, man-introduced species are referred to as adventive. Some of them naturalize, *i.e.*, can accomplish their full cycle without special protection. Others are sporadic, have low vitality. Others still owe their subsistence to the immediate protection of man: they have to be sown or planted in specially prepared soil, competition from other plants must be repeatedly eliminated; some of them must receive more moisture than the local climate provides, etc. In other words, each species shows a more or less complete adaptation to a given environment, which can be estimated in terms of origin, vitality and aggressivity (Hamel et Dansereau 1949).*

On the other hand, the *vegetation consists of a definite quantitative representation of the species available in the local flora.* Abundance will depend on many factors: *requirements, tolerances,* and capacity of utilizing environmental resources (space, air, light, heat, water, soil), in other words, *efficiency.* Limited requirements, extensive tolerances, high capacity for "making the best of" the resources will allow many species to occur in the flora and yet allow only a small number (especially in cold and temperate climates) to dominate the community of which they are a part.

Since quantitative representation, therefore, is the important criterion in the *description of vegetation,* a long list of species, to say nothing of a complete *enumeration of the flora,* are of little value. Instead, the *dominant* and some other *characteristic* species, must be recognized because of their *physiognomic prominence* and their *indicator value.* A knowledge of the *flora* will allow a classification of its species into floristic ele-

[4] I have attempted to develop this point of view in detail (unpublished, *loc cit.,* (a)).

* I have discussed elsewhere the degrees of indigenism (Dansereau, 1949b). Evidently, a certain population (even if derived from non-indigenous stock) can have crossed one or more specific or infraspecific thresholds after its original access to the area it now occupies.

ments of common origin (Flahaut: *in* Coste 1901; Fernald 1925, Marie-Victorin 1929, Braun-Blanquet 1937, Hultén 1937, Wulff 1943, Dansereau 1945, Raup 1947, Raymond 1950); a knowledge of the *vegetation* will premit an entirely different classification based on ecological requirements and usual rôle of the plant individuals in the landscape. *The former are historical indicators, the latter ecological indicators.*

The foregoing distinction may appear to be so simple as to be generally recognized. But such has not always been the case. For instance, Cockayne's (1921) admirable "Vegetation of New Zealand" and Marie-Victorin's (1935) preface to his monumental "Flore Laurentienne" do not actually convey spatial pictures of vegetation but are centered upon floristic considerations. Thus, the literature abounds in so-called regional description of vegetation which is in point of fact an enumeration of floristically significant species, characteristic of certain areas but not of their ecological functions or of their physiognomy.

The custom, therefore, of alluding to a vegetation type as "sedge meadow," "pine forest," "cypress swamp," "leather-leaf bog" implies that a certain species (of *Carex, Pinus, Taxodium, Chamaedaphne*) is dominant or is at least the most conspicuous plant. These summary expressions have long been current and are still in common use in manuals, floras and botanical literature in general. They figure on herbarium labels and serve to show in what terms the great majority of plant collectors think of ecological conditions.

However, the identity of the most apparent species is not alone involved in such designations. It could be argued that the relative poverty of temperate floras (as compared to tropical) and the familiarity of the dominant species even to the layman has made their names a short-cut reference to structure and function, which are really implicit. "Sedge meadow" means: small grass-like plants growing in tufts, losing their leaves in the fall, the renewal buds buried among the dried persistent bases of old leaves. "Pine forest" means a stand (of indeterminate density!) of rather tall trees with bunched, needlelike evergreen leaves. "Cypress swamp" is a flooded forest dominated by *Taxodium distichum* (not a *Cupressus!*), a buttressed tree with deciduous branchlets. "Leather-leaf bog" is an open expanse with dense growth of *Sphagnum* moss under a small semi-deciduous much-branched sub-shrub.

To many biologists as well as geographers, it will seem less important to thrash out the taxonomic affinities of these plants or their floristic relationships than to define accurately their structure and function or periodicity. For instance, the sedge *Carex crinita* is a member of the family Cyperaceae which ranges throughout the world, of the genus *Carex,* also almost universal but favouring moist-cold areas and including species in all kinds of habitats. Jack pine or *Pinus banksiana* is limited to cold parts of eastern North America, is closely related to the Appalachian *P. virginiana,* to the western North American *P. contorta,* to the European *P. sylvestris.* Other pines in the same areas also form forests, have other taxonomic affinities, a different distribution pattern, and range from wet to dry and from warm to cold sites and climates. Moreover, pine formations range from very open (*P. monophylla*) to park-like (*P. ponderosa*) to closed (*P. strobus*); also from very tall (*P. lambertiana*) to very short (*P. cembra*). The swamp cypress is related to the California redwoods and the Chinese dawn redwood; in pre-glacial times, the cypress occupied much of the Northern hemisphere, extending to Europe and Asia. As for *Chamaedaphne calyculata,* it is a monotypic species of the large family Ericaceae (*Rhododendron, Gaultheria, Kalmia, Arbutus,* etc.).

All the above contributes little to a clear description of the various associations involved. Ecologically, the sedge

has more in common with *Calamagrostis canadensis* (Gramineae) or *Chelone glabra* (Scrophulariaceae) with which it grows than with most other species of *Carex*. The pine is ecologically more closely related to the aspen (*Populus tremuloides*, Salicaceae), to the sweetfern (*Comptonia peregrina*, Myricaceae) or to a certain goldenrod (*Solidago puberula*, Compositae), its associates, than to the much more mesic white pine (*Pinus strobus*), even less to the southern loblolly pine (*P. taeda*) or the subtropical *P. caribaea* or *P. cubensis*. It is true that some of the other members of the ecological mosaic dominated by *Chamaedaphne* are also Ericaceae (*Kalmia angustifolia, Ledum groenlandicum, Vaccinium oxycoccos*), but the same region contains other members of that family in entirely different habitats, such as *Eriodendron arboreum* in the deciduous forest, *Moneses uniflora* in the spruce forest, etc.

Another essentially floristic approach to the classification of vegetation consists in mapping species and establishing areas of high coincidence. This method unquestionably brings to light very real affinities of origin and past history of a certain stock of species. For instance, Raup (1947) has given a very illuminating geographical analysis of the Canadian arctic flora and has brought out the factors which have influenced its evolution. His maps show that the living species of that flora fall into a restricted number of categories, each one of which is essentially an areal response to past vicissitudes. On an even broader scale, Hultén (1937) has provided a very convincing picture of the evolution of quaternary floras in glaciated boreal lands. This, however, does not permit a description of the present vegetation, even if the range of a species does give a clue to its indicator value.

Description of vegetation is always drawn from communities of plants, whether one thinks in terms of Warming's (1909) large units, of Weaver and Clements' (1938) regional units or of Braun-Blanquet's (1932) *association*, which is definable by its statistical floristic composition, its stratification and its dynamic status.

Therefore, it seems to me difficult to follow those authors who would define vegetation zones mainly by coinciding areas of species. Nichols' (1935) outline of the "White pine-Hemlock-Northern Hardwoods" region is largely based on such a criterion and underlines coincidence between floristic, bioclimatic and vegetation areas but does not actually define or describe the latter. Since Schouw's time (1823), several attempts have been made to classify "natural areas" by an indicator plant (mostly a tree) whose geographic boundaries were taken to be bioclimatically significant (de Martonne, Chevalier and Cuénot 1927). It has inevitably appeared, however, that the limits of a species and that of an association of which it is a part, not to mention that of a given climax-association (*sensu* Weaver and Clements 1938), rarely coincide. Where genera, instead of species are involved, as is often the case for instance in Merriam's (1898) life zones, the real relation to vegetation units is even more remote. Dice (1943) has recently published a classification of the "biotic provinces" of North America. Stress on the distribution of mammals has led him to draw some of his frontiers through areas of quite homogeneous vegetation. (Such are the southeastern limits of his *Canadian* zone.)

In the case of the deciduous forest of eastern North America, it is clear that the area of such species as the sugar maple, the white oak, the hickories, the yellow birch, and the chestnut very much exceeds that in which they are authentic components of the prevailing climax (Braun 1950).

This is not to say that floristic areas and classifications present no interest. Certainly, Drude (1890), Engler (*in* Diels 1936), Gaussen (1933), Dice (1943) and Good's (1947) classifications

are excellent, but they are devised for the purposes of historical biogeography. Only in a loose way do their subdivisions approximate vegetation units. Hayek (1926) has included in his book two maps, one of flora and the other of vegetation, as he seemed to feel rather more keenly than many students of floristics the considerable difference in point of view between the two types of study.

Cain (1947), however, has warned us against "compartmentalization in geographic thought." He claims that any phytosociological unit must be wholly contained within one floristic area.

To be sure, a combined attack of geobotanical and phytosociological techniques is most valuable. Cooper (1922) and Billings (1949) have proceeded in that way and their work brings into very sharp focus the relative narrowness of the chaparral and shadscale communities, respectively, as contrasted with the overlapping geographical areas of a small number of characteristic species. It would seem that the joint functions assumed by these species in their common area is a result of their fitness to a certain ecological optimum not encountered in the rest of their range.

Life-forms

A radical departure from taxonomic thinking in ecology was made by Raunkiaer (1934)[5] to whom the current concept of life-form must be credited. Du Rietz (1931) has shown the filiation of Raunkiaer's system and has, indeed, given an excellent and complete review of the classifications of plants on an adaptational basis. His own system consists of a very large number of subordinate categories. Several authors have somewhat modified the Raunkiaerean system, but on the whole the original framework has been retained largely because it is easy to apply (Cain 1950).

What it purports to do is to provide a small number of categories into which all plants can be fitted according to their apparent morphological-physiological response to the unfavourable season whether that be dry or cold. Of paramount importance is the *position of the perennating bud,* which permits six main classes to be recognized (fig. 1) as follows:

Phanerophytes, buds exposed to the full impact of climatic factors, being situated high above ground level: trees, shrubs. (Examples: *Acer rubrum, Cornus florida, Bertholletia excelsa, Larix europaea, Adansonia digitata.*)

Chamaephytes, buds close to the ground, under the influence of the soil area, protected by snow (if any) in winter: subshrubs, creeping herbs and woody plants. (Examples: *Lycopodium clavatum, Vaccinium vitis-idaea, Mitchella repens, Cassia uniflora, Vinca minor, Dacrydium laxifolium.*)

Hemicryptophytes, buds at soil-surface, annual growth dying down to that level: herbs of different types, growing in tussocks, rosettes, tall leafy stalks, etc. (Examples: *Aster acuminatus, Fragaria virginiana, Carex plantaginea, Andropogon virginicus, Sanicula europaea, Lobelia anceps.*)

Geophytes, buds below soil surface: many rhizomatous, tuberous and bulbous herbs. (Examples: *Trillium grandiflorum, Claytonia caroliniana, Smilacina racemosa, Ipomaea littoralis, Convallaria majalis, Iris xiphium, Lilium philippense.*)

Hydrophytes, buds permanently under water: all true aquatics. (Examples: *Sagittaria latifolia, Potamogeton alpinus, Nymphaea tuberosa, Eichhornia crassipes, Vallisneria spiralis, Zostera tasmanica.*)

Therophytes, buds contained in a seed: annuals. (Examples: *Polygonum convolvulus, Poa annua, Euphorbia brasiliensis, Cenchrus echinatus.*)

Each one of the foregoing has been variously subdivided (Fassett 1930, Du Rietz 1931, Braun-Blanquet 1932 (see table VII), Raunkiaer 1934, Dansereau

[5] Original publication 1904. Raunkiaer's work referred to here is the 1934 English translation.

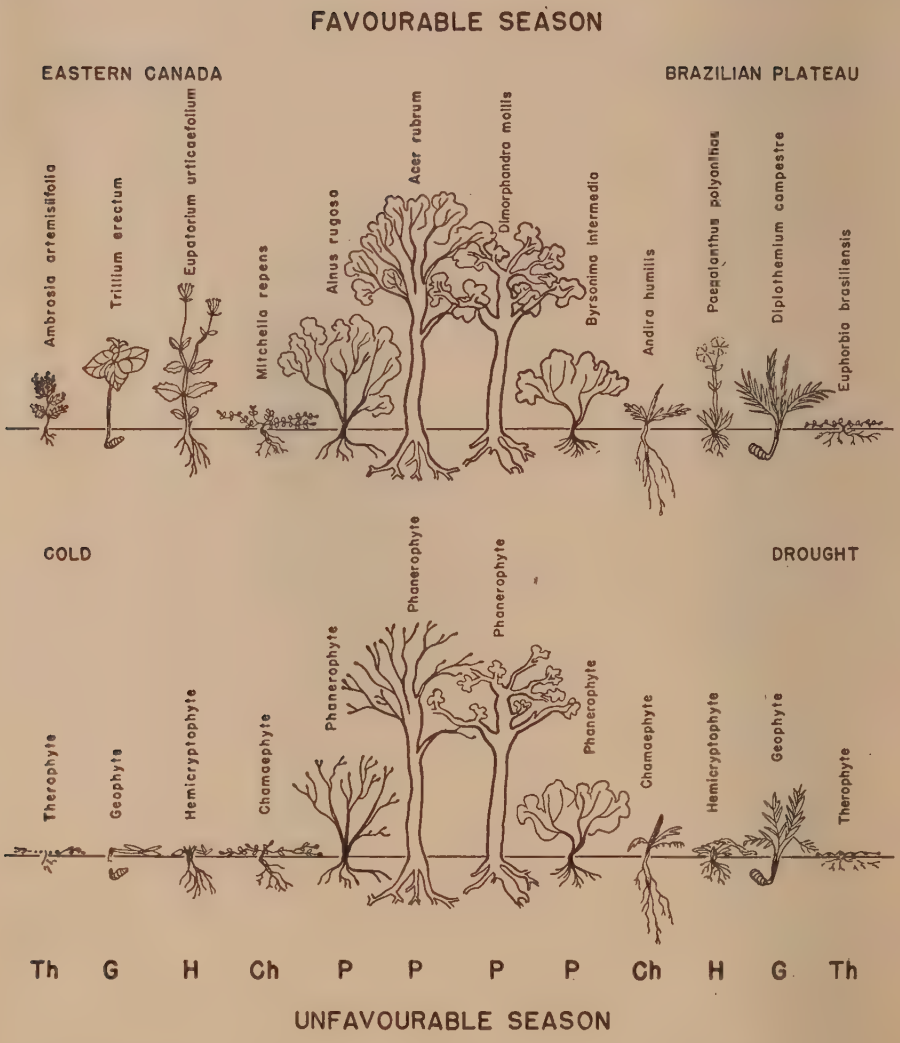


FIG. 1. Life-forms according to the Raunkiaer system and showing the appearance of the plants during the growing season (above) and during the unfavourable season (below). The latter is dominated by cold (left) or drought (right). Examples are taken, respectively, from the floras of Eastern Canada (left half) and of the Brazilian Plateau (right half).

1945) according to further adaptive modifications.

By submitting any *local flora* to the test of these criteria and by establishing the *percentage of the species* belonging to each one of the above categories, a biological spectrum is obtained, such as those appearing in table I.

The surprising feature in Raunkiaer's life-form system is that it should show such close correlation with major climatic units (for instance in terms of the Köppen classification) in spite of being essentially floristic, as generally applied by Raunkiaer, and not vegetational. As a matter of fact, a rare species, a common one and an abundant one all rate the same in a biological spectrum. It has been repeat-

edly pointed out (*e.g.*, by Braun-Blanquet 1932) that a quantitative coefficient would give further precision for describing vegetation. Such coefficients however have been little used and then only to relate to small areas (Raunkiaer 1934, Cain 1944, Dansereau 1945, Buell and Wilbur 1948). In spite of this shortcoming, the biological spectra which we do have are evidently significant. The implication, at present, is that greater and more widespread use of this method will yield valuable results (Cain 1950). For instance, it is most desirable to draw isobiochores —or lines joining localities of essentially identical biological spectrum. However, the use of spectra is not of universal applicability for the time being (as we do not possess a dense enough web of local floras, except in some parts of Europe), and it would be more than difficult to draw isobiochores over any large portion of the world.

In fact, life-forms and biological spectra lend themselves to a complex interpretation of the areas from which they were plotted. If we are to appreciate their full significance, we can hardly project them in a single direction: we must not assume a linear order from the phanerophytes to the therophytes. In warm moist environments phanerophytes dominate, in

TABLE I. *A selection of biological spectra in different parts of the world, illustrating similar responses to the main climatic control and minor responses to secondary factors. The symbols refer to Raunkiaer's (1934) life-forms:* P (*phanerophytes*), Ch (*chamaephytes*), H (*hemicryptophytes*), G (*geophytes*), HH (*hydrophytes*), Th (*therophytes*). *For further explanation see text, page 177. Where no figure appears under* HH, *they have been included in* G. *Most important life-form values are printed in boldface and italics.*

Climate (Köppen) in relation to Raunkiaer's life-forms		Area	Schimper and von Faber's types	Rübel's types	Raunkiaer's life-forms					
					P	Ch	H	G	HH	Th
		World or normal (1,000 spp.) (Raunkiaer 1934)			46	9	26	4	2	13
P	Afi	Seychelles (Raunkiaer 1934)	1	1	**61**	6	12	3	2	16
	Afwi	St. Thomas and S. Jan (Virgin Islands) (Raunkiaer 1934)	1	1	**61**	*12*	9	3	1	14
	Afwi	Sandy Point (Danish W. Indies) (Raunkiaer 1934)	1	1	**74**	*16*	4	1	0	5
Ch	E	Alps (Switzerland) (Braun-Blanquet 1932)	14	9	0	**24.5**	*68*	4		3.5
	E	Spitzbergen (Braun-Blanquet 1932)	14	9	1	*22*	*60*	*15*		2
	E	Eastern Canadian Arctic (Desmarais 1945)	14	9	0	**26.3**	*56.9*	*11.1*	3.7	2.0
H	Dfc	Central Switzerland (Braun-Blanquet 1932)	5	7	10	5	**50**	*15*		*20*
	Cfb	Paris area (Braun-Blanquet 1932)	5	7	8	6.5	**51.5**	*25*		9
	Dfb	Connecticut (Ennis 1928)	5	7	15	2	**49**	*22*		12
Th	BSks	Death Valley (Braun-Blanquet 1932)	13	6	*26*	7	18	2	5	**42**
	BS	Cyrenaica (Raunkiaer 1934)	13	6	9	14	19	8	0	**50**
	BS	Libyan desert (Raunkiaer 1934)	13	6	12	*21*	20	4	0	**42**

warm-dry areas therophytes are in the majority, whereas hemicryptophytes are numerous in moist and cool or cold regions (table I). The specialization of chamaephytes and geophytes is by no means so clear-cut. At all events, since all life-forms are present in almost all biological spectra, each one must be considered. It is not enough to describe the climate of the Lowlands of Switzerland as hemicryptophytic because that life-form attains the highest absolute percentage and shows the greatest departure from its percentage in the "normal" spectrum. One is also led to ascribe to the former Central European invasions and to recent disturbance a greater-than-normal representation of therophytes. In the same way, the Laurentian maple forest owes its high percentage of chamaephytes to its contact with Canadian forest (Dansereau 1943, Cain 1945). The high percentage of chamaephytes in the Libyan desert can likewise be ascribed to nearby Mediterranean influence.

Therefore, a classification of areas according to the life-forms of their floras is essentially a bioclimatic one, and the predominance of a certain life-form can be superimposed upon world climatic patterns, as will be shown in figure 6. A comparison of this figure with figure 5, built according to the same principles, shows that there is some lack of accord between floristic and ecological dominance, as floristic spectra cannot provide a picture of the actual structure of vegetation. The hemicryptophytic climates, for instance, are largely forest areas. Like Köppen's C and D climates, they cut clear across forest and prairie (Dansereau and Gille 1949).

That is not to say, however, that biological spectra do not show differences between prairie and forest areas, between cooler and warmer areas, especially within the same Köppen climatic belt. In fact, one of the most interesting applications of life-form statistics is that used by Raunkiaer himself (1934) to emphasize such climatic gradients as altitude and latitude, an increase of which is accompanied by a gradual decrease of phanerophytes, therophytes, geophytes and increase of hemicryptophytes and chamaephytes (see also Cain 1945, 1950). There is proof here of a positive relationship to climatic factors, *so long as contiguous areas are concerned.* In such cases, the flora is essentially from the same stocks. When similar areas on different continents are compared, discrepancies appear as a result of the floristic non-quantitative approach. For instance, the phanerophytic index of forest areas in Europe is lower than that of North America, glaciation having drastically impoverished the woody flora of Europe (Braun-Blanquet 1937, Dansereau 1943).

And now, how do *plant communities* compare when measured by biological spectra? It is at first hand evident that even then no direct reflection of structure is emphasized: even if similar associations (*e.g.*, belonging to an equivalent successional stage) in areas fairly alike, are compared, the actual quantitative distribution in space of the different life-forms can hardly be deduced, unless quantitative measurements are used, as Raunkiaer (1934), Cain (1944), Dansereau (1945), and Buell and Wilbur (1948) have done. Related associations belonging to the same sere show definite gradients which can be related to the "improvement" or "deterioration" of a certain factor (accumulation of humus, deepening shade, increased water-storing capacity). Raunkiaer (1934), and Dansereau and Gille (1949) have published data which indicate this in a pasture succession.

The life-form concept and system, therefore, are presumably best suited to bioclimatic analyses of the prevailing flora of an otherwise homogeneous area.[6] They do not bring forth a picture of what

[6] It is well to note that the existing spectra do not always refer to areas of homogeneous climate and vegetation. They are often calculated from lists of plants of a country, state or province with biologically unnatural boundaries.

TABLE II. *Huguet del Villar's (1929) classification of habitats, an ecological, non-geographical system*

ECOPHYTIA	Environment totally or partly aquatic HYDROPHYTIA (Holohydrophytia + Helophytia)	Harmony of factors			*Limnophytia*
		Dominant discrepancy of one factor	Chemical	Alkalinity	*Halohydrophytia*
				Acidity	*Oxyhydrophytia*
			Thermic	Excess	*Hydrothermophytia*
				Deficiency	*Cryophytia*
			Biotic	Mephitic accumulations	*(*Hydrosaprophytia*)
	Environment emerged PEZOPHYTIA (Lithophytia + Chasmophytia + Edaphophytia)	Harmony of factors	MESOPHYTIA	Constant	*Hygrophytia*
				Subconstant	*Subhygrophytia*
				Discontinuous	*Tropophytia*
		Dominant discrepancy of one factor	Water scarce XEROPHYTIA	Moderately	*Mesoxerophytia*
				Extremely	*Hyperxerophytia*
			Temperature extreme	Excess	*Subxerophytia*
				Deficiency	*Psychrophytia*
			Reaction diverging from neutral	Alkalinity	*Halophytia*
				Acidity	*Oxyphytia*
			Physical condition unfavorable	Substratum excessively loose	*Psammophytia*
				Substratum excessively dry	*Chersophytia*
				Substratum excessively compact *Petrophytia*	*Chasmophytia*
				Substratum excessively compact *Petrophytia*	*Lithophytia*
			Pertubing biotic factor	Putrescrible accumulations	**(*Pezosaprophytia*)
				General transformation of the environment	*Biogenophytia* (s. stricto)
				General transformation of the environment	*Paranthropophytia*
SAPROPHYTIA	Aquatic				**Hydrosaprophytia*
	Emerged				***Pezosaprophytia*
BIOPHYTIA	Exterior to biological activity				*Ectobiophytia*
	Affecting biological activity				*Endobiophytia*

the prevailing vegetation (as encompassed within its climatic limits) looks like and is made of. When applied to individual associations, it remains almost meaningless if quantitative factors (*e.g.*, frequency or constancy or mean abundance, etc.) are not used. Identification of all the species involved is necessary to the grading of life-forms and considerable quadratting is required to find the phytosociological coefficients. Needless to say, this can be done only by botanists with a specialized training. Therefore, biological spectra, for the time being, will prove extremely useful as a control of other systems of climatic recording and classification, but some more readily manageable units must be used in universal or broad regional mapping, and also for the representation of particular associations.

Ecological Classifications

There have also been classifications on an ecological basis, transcending regional differences and focused upon actual *habitat*. These systems are essentially causal and reflect an order of determining factors of decreasing biological significance. Huguet del Villar's (1929) will serve to illustrate this point. Table II shows the hierarchy of factors which he considers to offer the best expression of actual processes of adaptation. The 24 resulting categories can be said to lead to the principal types of habitat, but they hardly define in other than physical terms the major influences at work in the habitat, and not the kind of vegetation which one can expect to find therein.

Structural-physiognomic Classification

The need for physiognomic as opposed to taxonomic description of vegetation has long been recognized. Schimper (1903), and Warming (1909) described equivalent formations based on similarity in appearance and function of botanically unrelated dominant or characteristic species. These criteria represent *an appreciation of vegetation and not of flora,* although much of the vocabulary involved retains some preoccupation with phylogenetic affinities and the purpose of showing as much symmetry as possible in the analogy.[7]

The more recent systems of Rübel (1930) and Schimper and von Faber (1935) are freer from such preoccupations. They cover the most important types of plant formations to be found anywhere, afford the possibility of subdivision into many facies, and do not depend in any way upon either botanical composition or dynamic status.

According to Rübel, for instance, the *Laurisilvae* may or may not contain members of the family *Lauraceae,* but imply dominance of broadleaved evergreen woody species of a kind typified by the laurels, but which occurs in other genera and families (*Nothofagus, Arbutus,* etc.). The main criteria are woodiness, leaf shape and type, deciduousness. Both form and function are fairly evident in his first 19 categories. All of these are represented in different parts of the world. Most of them occur as climax somewhere. The following eight (nos. 20–27), however, are not characterized so much by the vegetation, which is always discontinuous, as by the physical factors of the environment itself. This shift in the criteria breaks the symmetry of the classification.

In spite of its apparent rigidity, such a scheme has provided a very convincing picture of vegetation types the world over. It brings together formations of similar build and function from widely separated areas. Some of these approximations will seem a little forced (the "Koniferen-Lorbeerwälder," for instance, included in the *Laurisilvae*), but on the whole these

[7] Very much has been made, especially by European phytosociologists, of the supposed equivalence between taxonomic (genera, species, subspecies, varieties) and ecological categories (orders, alliances, associations, sub-associations, facies, see Braun-Blanquet 1932, Etter 1943). The stressing of this analogy may be responsible for some of the existing confusion in defining units.

categories can be deemed true biological units.

In some ways and for some areas, Schimper and von Faber's (1935) map is more satisfactory. Their inventory of world vegetation is also more complete. Table III shows corresponding designations of formation-types, climates and life-forms.

More recently, Burtt-Davy (1938), faced with the difficult problem of a preliminary classification of tropical vegetation where detailed surveys and complete floristic inventories were not available, revised Schimper and Warming's physiognomic systems and also the excellent work of Tansley and Chipp (1926), and Champion (1936). Since then, Richards, Tansley, and Watt (1940), Beard (1944), and Gillman (1949) have made a further effort in this direction. All of these papers point to the increasing consciousness of *structure* as a significant factor in describing vegetation types. The papers cited above attempt only secondarily to relate structure to ecological factors and much of the nomenclature and procedure proposed emphasize this.

Richards, Tansley and Watt (1940) submit 22 features which should be investigated (in a tropical forest, the most

TABLE III. *The formation-types of Schimper and von Faber (1935), and their meaning in terms of climate, vegetation and flora. The structural differences are shown in various figures by the means of the new system proposed in this paper. The contacts between one type and one or more others in Schimper and von Faber's map illustrate the possible transitions, exchanges and genetic derivations. The confinement of a type within one or more of Köppen's climatic areas shows a more or less narrow climatic limitation. The life-forms are Raunkiaer's (1934). See text, page 177 and also figures 1, 5, and 6*

Formation-type of Schimper und von Faber	Type from which derived	Contacts with other types	Principal climatic types (Köppen)	Typical area where formation well developed	Illustration in present paper (no. of fig.)	Dominant life-form	
						of flora	of vegetation
1. Tropical rainforest	1	2, 3, 6, 8, 10, 13, 14	Af	Amazon	15	P	P
2. Subtropical rainforest	1	1, 3, 4, 6, 7, 8, 9, 10, 11, 14	Af, Aw	New South Wales	15	P	P
3. Monsoon forest	1, 2	1, 2, 6, 8 ,10	Am	Indo-China	15	P	P
4. Temperate rainforest	1, 2	2, 5, 7, 8, 10, 14	Cw, Cfb	New Zealand	16	H (P)	P
5. Summergreen deciduous forest	4	2, 4, 6, 7, 8, 9, 11, 12, 14	Cfb, Dfa	Eastern United States	14	H	P
6. Needle-leaf forest	4	1, 2, 3, 5, 7, 8, 9, 11, 12, 13, 14, 15	Dfc	Canada	12, 14	H (Ch)	P
7. Evergreen hardwood forest	2, 4	2, 4, 5, 6, 8, 9, 11, 13, 14	Csb	Italy	17	H (Ch)	P
8. Savana woodland	3, 4, 5, 6, 7	1, 2, 3, 4, 5, 6, 7, 9, 10, 11	Awi	Nevada	17	H (Ch)	P-H
9. Thorn forest and scrub	7, 10	2, 6, 7, 8, 10, 11, 12, 13, 14	BShw	Northeastern Brazil	18	Th-P	P-Th
10. Savana	7, 8	1, 2, 3, 4, 8, 9, 11, 14	Awi, Awt	Senegal Central Brazil	18	H (Ch)	P-Ch
11. Steppe and half desert	8. 10	2, 5, 6, 7, 8, 9, 10, 13, 14, 15	BSk	Central United States	18	H	H-Ch
12. Heath	5, 6, 7	5, 6, 14	Cfb	Western Ireland	19	Ch-H	Ch
13. Dry desert	9, 10, 11	2, 6, 7, 9, 10, 11, 14	BWh	Southwestern United States	19	Th	Ch-Th
14. Tundra and cold woodland	6, 12	1, 2, 4, 5, 6, 7, 9, 10, 11, 12, 13, 15	E	Ungava	14	Ch	Ch-H
15. Cold desert	14, 11, 13	6, 11, 14	F	Temperate area highlands and Arctic	14	Ch	Ch

highly complicated type of vegetation) in order to furnish adequate description of vegetation. Their statement of principle reads as follows (p. 229): "Vegetation should be primarily characterized *by its own features,* not by habitat, indispensable as is the study of habitat for the understanding of its nature and distribution." Gillman (1949) also reports: "We set out to classify vegetation by vegetation and not by anything else that may or may not be closely correlated with it." I shall have occasion to refer again to these sentences as they very aptly express one of the main purposes of the present paper.

Küchler's system

The preceding systems all offer a fixed number of categories, which maybe do not give full expression to the complexity of vegetation. At the same time, it is desirable not to multiply indefinitely the number of types to anticipate all possible combinations. For instance, in Rübel's first 13 categories (except no. 7), there is always an alternation of tree and shrub formation under each leaf-type. This can probably be simplified.

As yet, no one had proposed an adjustable scale. This, Küchler has done (1947, 1949). Inspired by climatological classifications, especially Köppen's (1923), he was led to formulate a new system in which he uses four series of symbols that can be combined so as to show the important features of plant cover. Table IV repeats Küchler's 1947 system as recently modified by him (1949). It is immediately evident that much more can be shown at a glance by this symbolism than will appear in Rübel's categories.

Considering Küchler's system, the following comments can be made.

Concerning the major divisions (or capital letters).—Five alternatives of woody types are designated. Breadth of leaves and deciduousness are the basis for divisions, but although two combinations of deciduous and evergreen species are foreseen, there is no category in which all the plants are semideciduous. Such a case does occur, for instance in tropical savana trees and in boreal bog shrubs. It also is unfortunate that categories *E* and *N* should be qualified as "coniferous" since quite a few Myrtaceae, Proteaceae, Rosaceae and others would fit into them. In fact it will be argued by some that the difference between needleleaf on the one hand and broadleaf on the other is no greater and no more significant than the differences between several categories which are here lumped under "broadleaf." Richards, Tansley, and Watt (1940) have found it useful to make such a distinction and to use Raunkiaer's (1934) leaf-size classes.

TABLE IV. *Küchler's physiognomic classification of vegetation (1949)*

CAPITAL LETTERS

Woody Vegetation:
- B: evergreen broadleaf
- D: deciduous broadleaf
- E: evergreen needleleaf (coniferous)
- N: deciduous needleleaf (coniferous)
- O: without leaves

Herbaceous Vegetation:
- G: graminoids
- H: forbs
- L: lichens and mosses

SMALL LETTERS

Group I: Height:
- t: tall; minimum height of trees: 25 m
  minimum height of herbaceous plants: 2 m
- m: medium tall; trees: 10–25 m
  herbaceous plants: ½–2 m
- l: low; maximum height of trees: 10 m
  maximum height of herbaceous plants: ½ m
- s: shrubs; minimum height: 1 m
- z: dwarf shrubs; maximum height: 1 m

Group II: Density:
- c: continuous growth
- i: plants usually do not touch
- p: woody plants scattered singly or in groves
  herbaceous plants in disconnected patches
- r: rare, yet conspicuous
- b: barren; vegetation largely or entirely absent

Group III: Special Features:
- e: epiphytes
- j: lianas
- k: succulents
- q: cushion plants
- u: palms
- v: bamboos
- w: aquatic vegetation
- y: tree ferns and tuft plants

The herbaceous categories have fortunately been revised to substitute graminoid for "grass" and to include lichens and mosses.

Concerning minor categories.—Group I. The symbols for height are one of the best features of the system, as they provide an excellent picture of vertical extension and thereby fix one of the spatial dimensions of vegetation. There would seem to be little profit, except in detailed local monographic study, in further subdividing. It may be questioned whether *s* and *z* are really necessary. Could not shrubs be fitted, as well as trees and herbaceous plants, into the three divisions *t, m* and *l*? In fact, it is not too easy to distinguish shrubs from trees in all cases. And since an essentially spatial descriptive scheme is set up, all the transgressive individuals are temporarily part of the lower strata. Richards, Tansley, and Watt (1940) emphasize this in their study.

Group II. The symbols of this group are meant to convey a picture of the horizontal spread or coverage of features mentioned above. All important differences seem to be provided for, although continuity in space and time are not clearly distinguished in category *c*. The difference between *i* and *p*, which may escape some plant-geographers, seems to me especially important. Such a scale could well be used to show stratification if any. However, in the author's own application of his system (Küchler 1949) this is not too explicit. For instance, how should one represent a larch stand with scattered semideciduous ericaceous shrubs, a continuous ground cover of sedges resting on *Sphagnum* moss? *Nmi* is for *Larix; Dzi* is for *Ledum* or *Kalmia;*[8] *Glc* is for *Carex* and *Lc* is for *Sphagnum.* Should the formula read *NmDziGlLc* or would it not be better to emphasize the synusiae as follows: *Nmi. Dzi.Glc.Lc?* In his second paper (1949), Küchler himself admits that periods could separate the synusiae. If this procedure is adopted, then should not each segment of the formula contain one capital letter and one letter each of groups I and II? It would seem that Champion's (1936) Indian deciduous forest, given by Küchler (1949) as *Dmls.jr.Gp.* has three synusiae (of undetermined coverage) in the first segment; one very sparse synusia (of indeterminate leaf-type) in the second; and a well-defined one as the third segment. As for the last formula given by the author in his second paper, *Btmlsej,* by which he shows stratification in lowland rainforest, it seems to imply that not only the canopy trees, but also smaller trees, shrubs (epiphytes and lianas?) are all broadleaved!

Another remark concerns symbol *r,* which stands for a "rare, yet conspicuous" feature. Inasmuch as it is already implied by the author that the order in which symbols of the same group appear indicates their relative importance, one will wonder whether this additional symbol is necessary.

Group III. This refers to eight more or less unusual life-forms which are not often dominant and are implied in the general scheme of this classification as accessory characteristics. Four of them, however, *k, u, v and y*[9] will occasionally be dominant in the vegetation as a whole and all of them can be so at least in one synusia. As for aquatic vegetation, it may prove desirable to contrast truly aquatic communities with those including a scattering of aquatic biotopes. But, aquatic plants range through many life-forms (Dansereau 1945) of varying significance. Moreover this symbol is somewhat at variance with the logic of the system as a whole which does not refer to

[8] These plants are really semideciduous and Küchler's 1947 system had provided a symbol (S) for them, although it was not clear whether he meant semideciduous formations or mixtures of deciduous and evergreen species.

[9] Categories *u* and *y* have been called *rosette trees* by Cuatrecasas (1949) who considers them as a single broad life-form, a view which seems quite logical.

environmental conditions but to "features of the vegetation itself"!

Küchler has entitled his 1947 paper "A geographic system of vegetation." The implication is that the symbolism he proposes as a parallel to the climatological one, is essentially aimed at small scale mapping and therefore applied to an overall description of regional vegetation rather than to a detailed characterization of individual plant communities. On such a scale, it may be sufficient, as he himself suggests, and has demonstrated (1948) to indicate the character of the upper layer of the vegetation (*e.g.*, trees of the forest), whereas, mapping on a larger scale could include reference to all layers present in each type of community. This has already been done by Küchler and some of his collaborators. Thus far, a map of Manchuria has appeared (Küchler 1948) and one of the Upper Peninsula of Michigan (Küchler 1950). In fact this system has such appeal that the latest issue of Goode's School Atlas (Goode and Espenshade 1950) includes a map of the vegetation of the world designed by Küchler.

Description of Vegetation

All such endeavours evoke the general problem of the description of vegetation. What should be considered first, second and last? How far can one simplify in order to present a synthesis? How far into structural details should one go? What should be mapped: what we think or know to have been the original vegetation or what is there today? Climax areas or the now prevailing subclimaxes and disclimaxes? In other words, a purely empirical account of things as they are, or an interpretation of the landscape? or some combination of both?

An ideal seems to have been realized in some careful and complete monographs such as Braun-Blanquet's (1936), Etter's (1943), Guinochet's (1939), Trochain's (1940), Lebrun's (1947). These are excellent because they combine many successive approaches and pose all the essential questions as to vegetation itself and its relation to environment. On the other hand, the wealth of factual information which they offer fully allows other interpretations to readers with a different scientific philosophy.

In fact, there are two different sets of problems: the first concerns actual *description* of vegetation whereas the second concerns the *relations* of vegetation. In reference to description, and to repeat a quotation given above (Richards, Tansley and Watt 1940): "Vegetation should be primarily characterized *by its own features. . . .*" Each one of these features must be investigated in order fully to characterize a community or an area. In this connection, it may be said that *the fundamentals of the description of vegetation relate to structure, function, composition and dynamics.* It will be worthwhile considering what these terms imply and what kind of variation is present in each case. No causal considerations need be introduced at all, as they do not actually bear on this purely descriptive phase.

Structure

Structure is the organization in space of the individuals composing a vegetation type or association. In other words, a definition of structure answers the question: what part of the cubic dimensions comprised between the extreme vertical and horizontal extensions of plants is occupied and how are the masses distributed? How many kinds of structure are there? The kinds of structure, or formations, fall into four main biochores: desert, grassland, savana, forest. Quite independently of their geographic and ecological significance (which will be considered below), these four major subdivisions offer the maximum of *structural contrast.* This is reducible to the following factors. *Desert* has open, discontinuous cover, considerable unoccupied (but not necessarily unused) space; *grassland* has no trees, but rather closed, often unistratal, low plant cover; *savana* may have

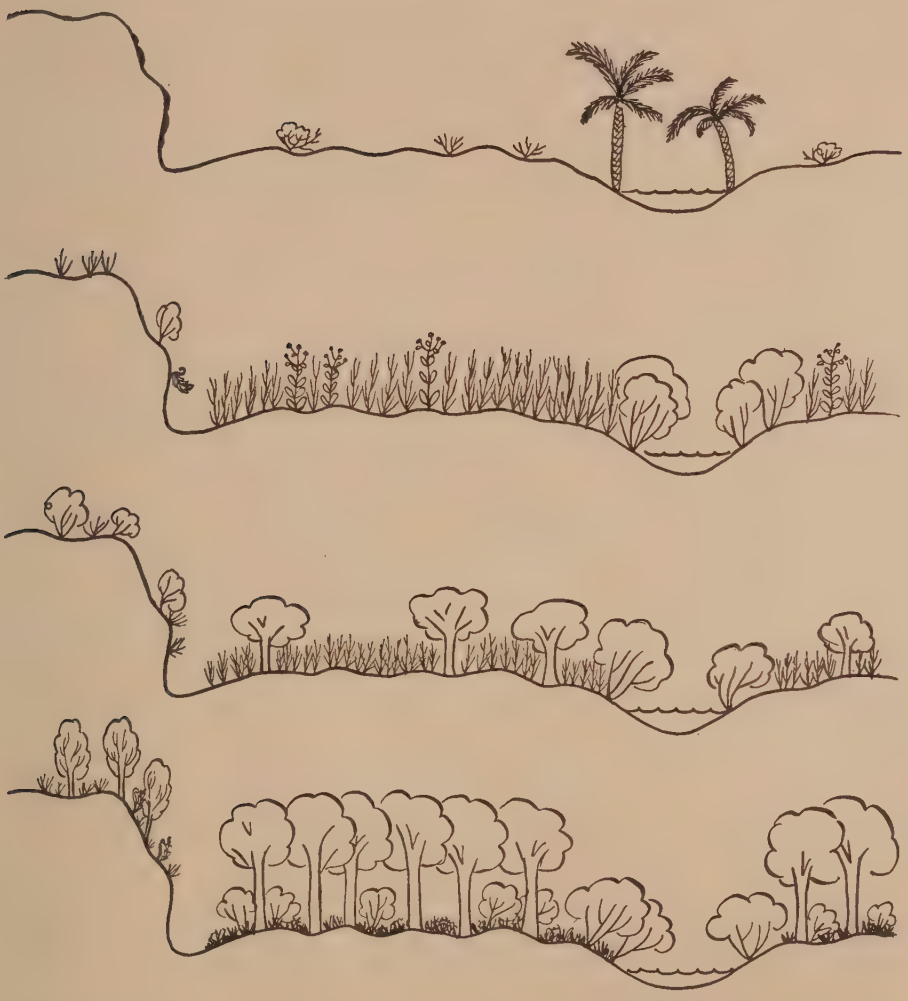


FIG. 2. Extremes of habitat within the four principal biochores (from top to bottom): desert, grassland, savana, forest. The center is occupied by upland and colonized by climax vegetation. Other features shown are: wind-beaten hill, cliff, floodplain.

a more or less closed ground layer, but always a very discontinuous upper (woody) layer; *forest* always has a continuous upper layer. These features appear in the middle portion of figure 2. (See also table V.)

Of course, each of these is further divisible into several types, for instance broadleaved, microphyll, needle-leaved forests; tussockland, steppe, tall-grass grassland, etc. This is still incomplete, however, as density must be registered and above all stratification: for instance, tall, close, needle-leaved forest with broad-leaved scattered deciduous shrub layer, sparse microphyll herbaceous layer and continuous moss layer. Further elaboration would include mode of branching of trees and shrubs and degree of overlapping of plants belonging to different life-forms. Structure has been represented as shown in figures 2 and 3, or in the sketch-

diagrams of Richards, Tansley and Watt (1940), Beard (1944), Egler (1947).

Function

Function is indicated as a time-factor inseparable from form (or structure) and sometimes implying seasonal changes thereof. *It essentially centres about the morphology, behaviour and duration of organs, or periodicity:* flowering and fruiting period for instance. But the greatest emphasis is generally placed upon the vegetative parts which are: evergreen, semideciduous, deciduous, or leafless.

In the majority of cases, external morphology corresponds to adaptive processes, although there are exceptions (xeromorphs which are not actually xerophytic, etc.). That is why many writers have graded local floras as to leaf size and shape (Raunkiaer 1934) and even leaf outline and serration (Bews 1927). Some even require to distinguish between pinnate and digitate compound leaves (Richards, Tansley, and Watt 1940).

No less important, it would seem, is leaf texture: the filmy frond of the Hymenophyllaceae, the membranous leaves of the nettle (*Urtica* spp.), the coriaceous leaves of the *Rhododendron* and the fleshy leaves of the stonecrops (*Sedum* spp.) are in strong contrast both as to form and function.

Composition

Composition is best shown by a complete list of all species present. The longer the list, however, the greater the difficulty of singling out the significant species, which must either be abundant or exclusive or serve otherwise as indicators of some relevant feature. Therefore, the list, if given, will take its meaning from the synthetic figures for frequency, presence, constancy and abundance (Braun-Blanquet 1932); or it will be reassembled into indicator-groups (Dansereau 1943). In fact, data containing that amount of precision (and including at least some of the quantitative notations mentioned above) can subsequently be simplified in various ways (Braun-Blanquet *et al.*

TABLE V. *The contrasting factors and resulting vegetation-type in the four principal biochores*

		Desert	Grassland	Savana	Forest
Precipitation	Quantity	Very low	Low	Low and variable	High
	Distribution	Sporadic	Uneven	Uneven, unreliable	Even or uneven
Availability of water		Torrential at surface, then washed to depth, stored	Available in depth	Stored in deep layers	Available at surface
Most abundant life-forms in flora		Th Ch	H	H (Ch)	H P
Vegetation period	Season	All year	Usually interrupted	Interrupted or slowed down	Interrupted to continuous
	Maximum growth	Spring or after rains	Summer	After rains	Usually summer
Flowering period		Very short, after rains	Throughout vegetation period	Throughout vegetation period; maximum after rains	Throughout vegetation period; maximum in summer
Trees	Ecological group	Xerophytic	Hygrophytic, mesophytic	Hygrophytic, xerophytic	Hygrophytic, mesophytic
	Habitat	Washes	Floodplain	Floodplain, upland	Floodplain, upland
Structure of upland vegetation	Tree layer	Absent or extremely open	Absent	Open	Closed
	Shrub layer	Extremely open	Usually absent or scattered	Bunched or scattered	Sparse
	Herb layer	Extremely scattered or bunched	Discontinuous to continuous to dense	Bunched to continuous	Generally sparse

1936–39), mapping included (Braun-Blanquet, Emberger et Molinier 1947).

Otherwise, only dominant, abundant or characteristic species *in each layer* will be considered. Such is the procedure followed in France by Gaussen (1947) and in California by Jensen (1947). It is almost inapplicable on small-scale maps, but is of course excellent on large-scale ones. Gaussen and Rey's (1947) beautiful vegetation map of Toulouse, (1 : 200,000) which was established with the means of this technique offers ample proof of that!

However, it is evident that no such scheme of universal applicability can be devised as one symbol is necessary for each species involved. Gaussen's "signes conventionnels" (1947) number no less than 432! and they contain a repertory which is inclusive only for France! It is not clear what use Jensen (1947) made of his elaborate symbols (one for each species) as his published maps are generalized and only show the single dominant.

Dynamics

Dynamics refers to *the seral position of an association:* is it a pioneer, consolidating, subclimax, quasiclimax or climax community? Is it a stage in the xerosere or the hydrosere or even a more narrowly limited association such as of the halosere, the psammosere, the limnosere? As a result of disturbance, is it a secondary pioneer or consolidation stage or a disclimax?

Not in all cases is it easy to apply such a classification. On dunes, in old fields and other places where the early stages of succession progress at an apparent pace, the relative position of each community is not too difficult to establish. However, later progress and the final edaphic and climatic checks on the entire process are much more complex and have sometimes been estimated "subjectively." The very real difficulties involved in the approach to this element of description does not make it biologically less significant, and imperfect and controvertible as they may be, it will be useful to set up categories in this respect.[10]

Let us now consider two examples: the sahuaro desert of southwestern Arizona and the jack pine barrens of Lake St. John (Quebec). Taking into account the four headings mentioned above, these two communities can be briefly described as follows (see fig. 3).

Sahuaro desert. Upper layer (15–30 feet high) of very sparse *Carnegiea gigantea* (40–60 feet apart); second layer 8–12 feet high, very sparse, with *Fouquieria splendens;* third layer (2–6 feet high, 6–10 feet between shrubs) dominated by *Larrea glutinosa;* also *Krameria parvifolia, Parosela mollis, Encelia actoni;* fourth layer (6 inches to 2 feet high, herbs and subshrubs about 5–10 feet apart), *Franseria dumosa* dominant; fifth layer, small annual herbs in patches, none of which is dominant: *Chaenactis carphocline, Gilia schottii, Nama demissum, Wahlenbergia albomarginata, Cryptantha parviflora, Eremiastrum bellidioides, Chorizanthe rigida.* The latter appear in the spring only and when there have been winter rains, then disappear entirely. The two upper layers are leafless except *Fouquieria* which sprouts its foliage for only a few weeks after rains. The third layer is evergreen and the fourth deciduous. This association is climax in its area.

Jack pine barren. Upper layer (10–35 feet high, spacing 25 feet between trees): *Pinus banksiana* and a very few *Betula papyrifera* var. *cordifolia* and *Picea mariana;* second layer (3–10 feet, spacing 10–25 feet), the same species, mostly jack pine; third layer (1–3 feet, spacing less than 2 feet): *Comptonia peregrina* dominant and a scattering of *Pteridium aquilinum* ssp. *latiusculum, Vaccinium canadense, Solidago puberula;* fourth layer 6 inches to 1 foot high,

[10] The underlying complexities and principles can hardly be discussed or even stated here. I have attempted to do so recently (unpublished, *loc. cit.,* (b)).

clumps about 1 foot in diameter, average spacing 6 feet: *Gaultheria procumbens, Lycopodium tristachyum.* The birch, sweet-fern, fern and goldenrod are deciduous, the rest evergreen. This association is a widespread fire disclimax in the area. Figure 3 is a rough sketch, such as is usually made in the field by ecologists.

Relations of Vegetation

The above merely describes two stands which may be fairly typical of whole associations. As such it is more or less static. On the other hand, *the fundamental relations of vegetation to environment concern area, climate, soil, animals, man and time.* These are the factors which most definitely limit the operation of associations and which must be investigated if an explanation of their present position is sought.

Area

Areal dimensions for living beings are included in the biosphere (Vernadsky 1945), that portion of air, land, and water which offers minimum conditions to the conservation of protoplasm. The relative density of the medium has allowed a first subdivision (ecological rather than geographic) into three *biocycles* (Hesse, Allee and Schmidt 1937): salt water, fresh-water and land (see fig. 4). World distribution of rainfall and temperature (*climate*) creates a geographic pattern to which vegetation responds by *formations* of essentially identical *structure.* These are the *biochores* of which four major types can be recog-

Fig. 3. The sahuaro desert of Southwestern Arizona and the pine barren of Lake St. John (Quebec) as sketched in profile, showing the essentials of structure and composition.

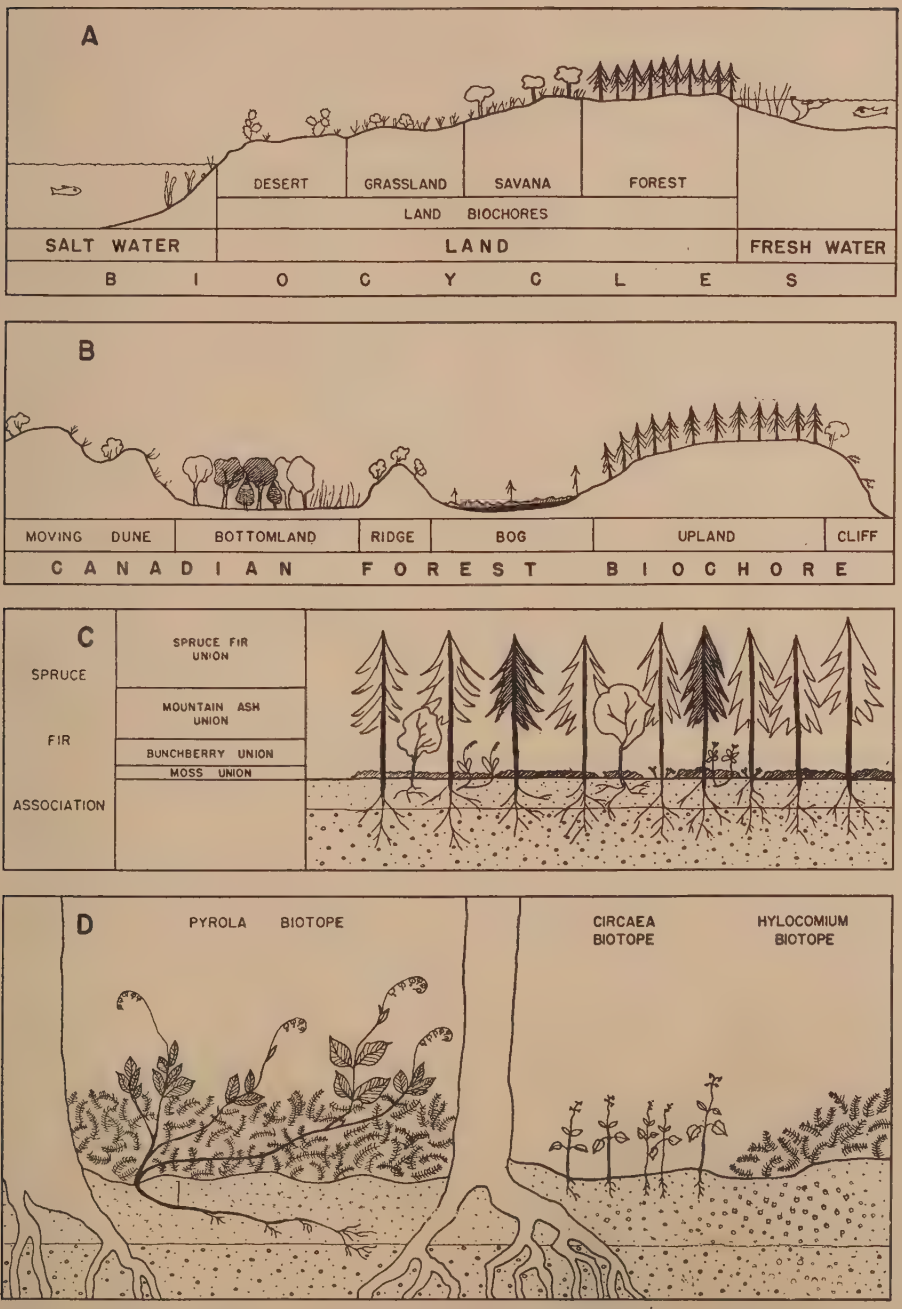


FIG. 4. The four principal orders of ecological integration. **A.** The biochores within biocycles. **B.** The habitats within a biochore. **C.** The synusiae within a community. **D.** The biotopes within a synusia.

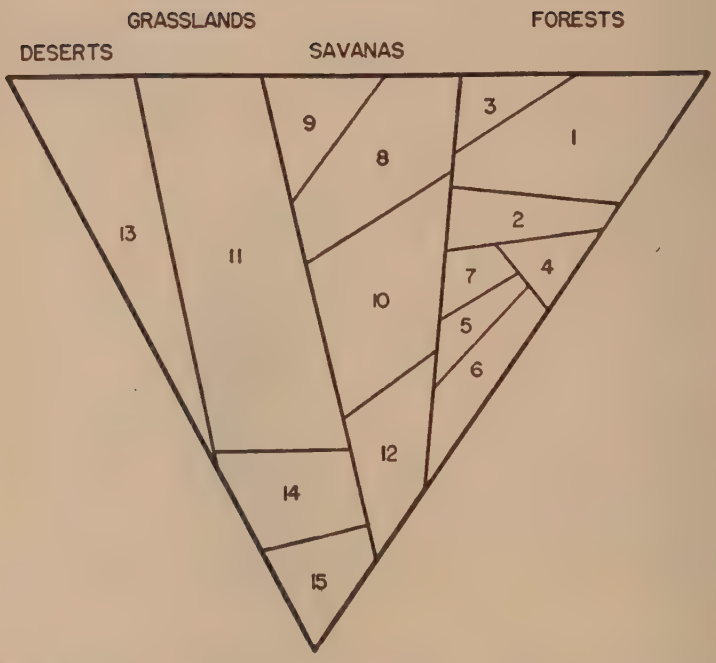


FIG. 5. A bioclimatic diagram arranged according to increasing temperatures (bottom upwards) and increasing rainfall (left to right). The plant formations are represented by a number corresponding to Schimper and von Faber's major types as enumerated in table III. Extreme of warmth and moisture is in upper right-hand angle; extreme of warmth and drought is in upper left-hand angle; lower angle is extreme cold and low precipitation.

nized: deserts, grasslands, savanas and forests (see above under "structure" and below, under "climate," and figs. 2 and 5). Within the limits of a biochore occur a number of *habitats,* ranging from the driest to the moistest possible under the limitations already imposed by climate, and largely due to *topographic conditions.* The topography therefore will determine how much of the biochore's mosaic will attain climax status, how much will be occupied by hydroseral, how much by xeroseral stages. The habitat, in turn, with its peculiar *microclimate* and its definite plant *association* may consist of one to many *synusiae* or layers occupied by plant *unions.* These are further reducible to a certain number of *biotopes* to which certain organisms or societies will be confined (mosses, lichens, insect larvae on the bark of trees, small moisture-loving herbs in wet pockets of an otherwise well-drained soil). In its relationships to area, therefore, vegetation undergoes the successive limitations of medium (biocycle), climate (biochore), topography (habitat), microclimate (association) and biological interference (synusia) and immediately operating physical and biological factors (biotope). For purposes of study and subsequent description, each one of these levels of integration of living beings and of communities must be well defined in terms of its physical, chemical and biological determinants. As the family, the genus, the species and the variety imply different orders of magnitude, so do the biochore, the association, the synusia, the biotope.[11]

[11] I do not use this analogy without some misgivings as I feel that some ecologists have shown a tendency to overstress it and eventually

The forces in operation, and the results achieved physiognomically, necessitate a different approach (and a different vocabulary) at each level.[12]

Figure 4 gives the example of *Circaea alpina,* a small annual plant which is generally quite gregarious and grows in patches at the foot of coniferous trees (mostly spruces and firs) on the well-aerated acid humus. It cannot compete with mosses, so that it rarely occupies large continuous stretches of the forest floor in a mature stand. What figure 4 shows are its successive limitations: A, to the *forest biochore,* a subdivision of the *land biocycle;* B, to *upland Canadian forest,* the climax *association* within that biochore; C to the lowest or moss *synusia* within that association and D to the *biotope* described above within that synusia. *Circaea alpina* is a land plant, of moist, cold, coniferous forest areas (Europe, Asia and America), that grows in the upland climax forest, in its lowest stratum, in disconnected colonies. It forms a community of a very low order (the "socies" of many ecologists) which can be integrated in at least three larger units; the union (at synusia level), the association (at habitat level), the formation (at climate level).

Climate

Climatic patterns are usually devised on the basis of a combination of temperature and rainfall means. The widely applied Köppen (1923) system, Thornthwaite's (1931) system, and still others do not always provide climatic boundaries that coincide with the limits of known climaxes or even biomes (sensu Clements and Shelford, 1939). In fact they sometimes do not even coincide with such broad biological units as biochores: the Central European and North American grasslands are not within the range of one given climatic type; in fact some climates (such as Köppen's Dfb) stretch clear across areas of deciduous and Canadian forest well into the heart of the prairie. Further examples of this are to be found in table III (nos. 2, 4, 5 and 10).

However imperfect the means of measuring climate, it would seem that climatologists recognize that the best indicators of homogeneous areas are the living beings themselves, and foremost the aggregates that compose natural vegetation. Vahl (*in* Reumert 1949) has given it a prominent place in his classification and Thornthwaite's (1948) recent modification of his own system clearly shows a growing concern with plant life. The new maps produced by these altered norms are much closer to significant biological limits (see, for instance, Hare 1950). Quite apart from the influence of climates on the distribution of individual plant species, climate strikes at the *structure* of vegetation everywhere in the same way, whatever its floristic *composition.* That is to say, *similar climates in widely separated parts of the world induce the emergence of similar kinds of plant formations in the physiognomic sense.**

It has been attempted, in figure 5, to encompass within a triangle the diverse conjunctions of the two most important meteorological elements, temperature (pictured as increasing from bottom upwards) and rainfall (pictured as increasing from left to right). This scheme does not rest on precise data which would probably have to include an efficiency co-

to forget that it is nothing more than a figure and does not really involve identical biological phenomena.

[12] I have attempted to fully develop and illustrate this idea elsewhere (Dansereau 1946a, 1949b, 1951a) and to register a plea for clearer thinking along these lines. See also Egler, 1942.

* I am aware that this statement cannot go unchallenged. A brief paper by Beadle (1951) draws attention to some faulty interpretations due to an indiscriminate application of this or a similar "law." As has been mentioned repeatedly above, all the principles accepted by some and rejected by others cannot be discussed in any detail. I would only state, for the moment, that Beadle's argument does not conflict as much as it would seem with the above statement.

efficient (see Thornthwaite 1948), but merely tries to show the relative position of the principal formations and their correspondence to a climatic constellation.[13]

A point which seems to be of some importance at present, is the recognition of four major formation groups of biochores of equal rank on the basis of structure and in utter disregard of composition: deserts, grasslands, savanas, forests.[14] Table V shows the principal features, climatic, edaphic and biological, which prevail in each one of these. It would seem that the gravity of both causal factors and resulting life conditions fully warrant the setting apart as primary of these four divisions.

Figure 5 shows how they can subsequently be broken up, on a world basis, into formation units. Schimper and von Faber's (1935) map of world vegetation may leave much to be desired, but is probably the best available for the time being and for the purpose at hand. Their numbers 1–7 are *forest;* 8, 9, 10 and 12 are interpreted here as *savana;* 11, 14 and 15 as *grassland* and 13 as *desert.* Reference to table III will throw further emphasis on the differences involved and will evoke concrete examples of what is implied.

The savana biochore as understood here will not meet with the approval of some geographers and phytogeographers who would restrict that term to what appears here as no. 10 or nos. 8 and 10. They will hardly endorse an extension of the term to include the oak woodland of California (Jensen 1947, Munz, and Keck 1949), a considerable part of the western yellow pine "forest," and even less the Hudsonian taiga or "lichen woodland" (Dansereau 1944, 1946a, 1948, Hare 1950). In fact these formations do not differ substantially *in structure* from the true African and South American savanas. As responses to climate itself, although they are situated in colder areas, they probably do not behave any differently either. I would like to suggest that the determining mode in climatic adjustment of savanas is the irregularity of fluctuations.

However that may be, on the grounds of structure alone, the formations listed here under savana are at least as much like one another as are those listed under *forest.* If it is the word savana that is employed in too broad a sense, I should be glad to have another substituted, but it seems to me that a major structural category is involved.

Figure 6 is offered as a parallel to figure 5 to show at once the discrepancies and the similarities of trend between vegetation and flora. On the world-climatic pattern of vegetation of figure 5 are superimposed lines, in figure 6, showing the limits of the life-form climates or phytoclimates (Cain 1950). Whereas savanas and forest areas are actually dominated by trees, only the warm moist areas have a very large relative number of tree species. At temperate latitudes, the hemicryptophytes dominate the flora of prairie, savana and forest alike. The chamaephytes predominate in the coldest areas, even in the deserts, whereas the therophytes are most numerous in the flora of warm-dry formations although they are not a permanent feature of the landscape.

This diagram may also introduce to the phylogeny of the life-forms which has presumably not operated in a linear sequence. This has already been suggested in a previous section and I have discussed it at greater length elsewhere,[15] together with the genesis and interrelations of

[13] A figure closely resembling figure 5 was first used in a general course of Biogeography which I taught at Universidade do Brasil, in Rio de Janeiro, in July and August 1946, and published in 1949 in its original form. I am encouraged in the procedure followed here by the publication of Holdridge's (1947) diagram where a quite similar system is outlined although with considerably greater precision.

[14] A thorough discussion of *transitions* and *ecotones* is certainly most desirable at this time and I hope shortly to offer a small contribution to the definition of these terms.

[15] Unpublished, *loc. cit.,* (a).

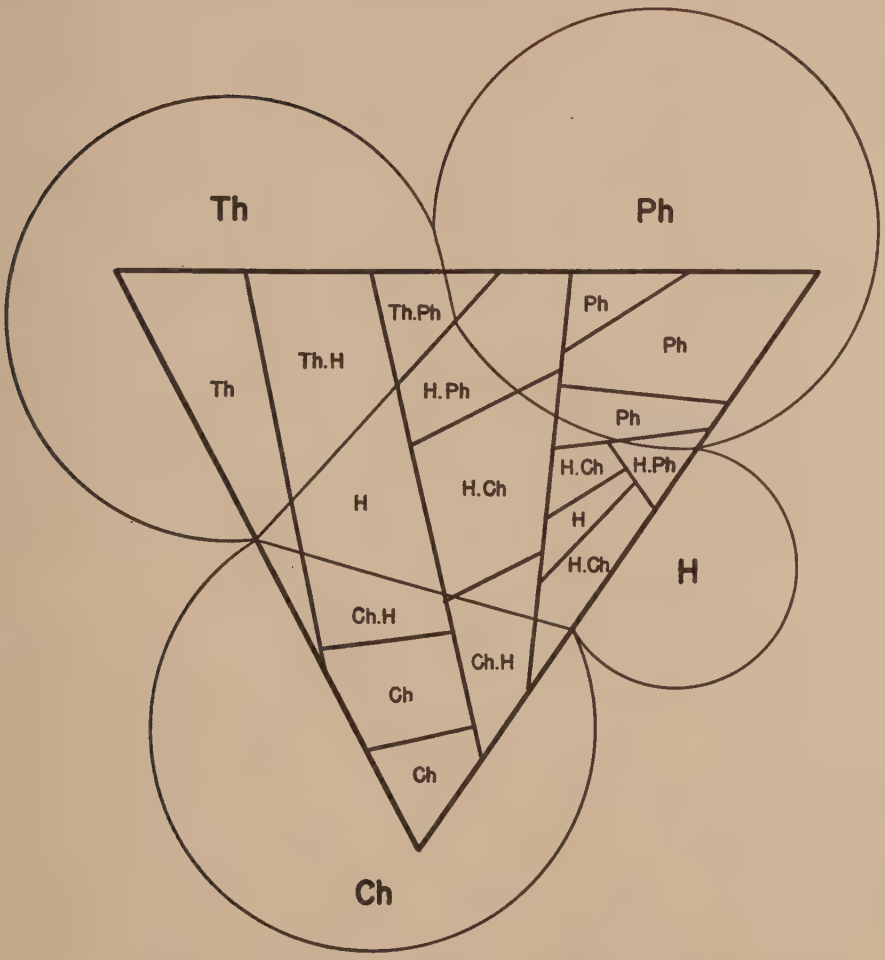


FIG. 6. Bioclimatic areas as characterized by the principal life-forms in the flora. For relation to vegetation compare with figure 5.

the plant-formations themselves wherein they originated.

Soil

Soil, especially if considered as a limiting factor, does not seem generally to bear on the distribution of climax vegetation, if not to introduce minor variants (*e.g.,* Etter 1943). It has long been maintained by many ecologists that climax vegetation, in structure and even in essential composition was independent of geological substratum and of soil (Braun-Blanquet 1932), inasmuch as the pedoclimax, or zonal soil, and the phytoclimax were products of a parallel evolution (Jenny 1941), the culmination of which was under the control of climate.[16] Con-

[16] Australian writers have not generally accepted this view and have, on the contrary claimed that the edaphic factor outweighed the climatic. See Tansley's discussion (1948) of Crocker and Wood's work. I have recently attempted to review this situation in terms of co-operating and disoperating ecological gradients in my unpublished manuscript, *loc. cit.,* (b). The entire and complex phenomenon can hardly be accounted for in the present paper. See also footnote on page 193 and Beadle 1951.

currently, it was recognized that pioneer and even later seral stages were much more sensitive to the selective influence of soil. It follows that a climatic area encompassing geological and physiographic variations, although it will bear an essentially uniform climax, will have different subclimaxes leading up to it and strikingly different pioneer stages. It also follows that after devastation of the climax over large areas, sharp differences in the vegetal cover may appear because of topography and soil and therefore break what was a homogeneous stretch into several seemingly distinct zones. Moreover, the extension of a subclimax that much exceeds that of a climax over two neighboring climax-areas, after man's interference, will lend a deceiving uniformity to two intrinsically distinct areas. Such is the case, for instance of the jack pine forest as mapped by Shantz and Zon (1923): parts of Michigan, Wisconsin and Minnesota are disputed ground between the tall-grass, oak-hickory, beech-maple and spruce-fir climaxes whose frontiers are at the present time obscured by areas of jack pine. Likewise, in the Canterbury Plain of New Zealand, much of the tussockland is secondary whereas some of it is climax and the delimitation has become very difficult (Zotov 1947).

Animals

There is some question as to whether animals in the wild state can exert a major controlling influence over virgin vegetation. Some examples come to mind, such as the bison in the North American prairie (Clements and Shelford 1939) that maintained a balance between tall, medium and low grasses. The moa may have played a similar rôle in the South Island of New Zealand. Both have affected the landscape to the point of extending the prairies or tussockland beyond their climatic limits. The large herds of herbivores that swamp African plateaus probably similarly extend the range of savana. Another instance is offered by Polunin (1949) who suggests that the large flocks of breeding birds in some parts of the arctic, by providing otherwise unavailable quantities of nitrogen, induce the formation of grassy swards instead of heaths.

Such cases must remain exceptional, however, and it is hardly known, at this time, what is the strength of their influence.

In already disturbed areas, of course, the picture can be quite different, especially if exotic species are involved. Rabbits and deer in New Zealand have completely changed the face of many landscapes. "Pests" (animal and plant) should also be mentioned in this connection: the spruce sawfly and the Japanese chestnut blight have deeply modified the structure of large tracts of the Appalachian forest.

Man

Man, as a disturbing agent, can hardly be disregarded, as he has for centuries tampered with the integrations and balances of nature. In many regions, he has so far upset primeval conditions as to make the reconstitution of primitive types very improbable, for instance, in dry areas such as northeastern Brazil, where the water-balance is so precarious.

Even an enumeration of the various ways in which man affects vegetation cannot be given here. It could be argued that the disturbance brought by him does not result in any processes different from those caused by "natural" agencies, but only the time-scale of operation. There is a good deal of evidence that that is not always so, whether one considers the genetic, physiological, ecological or geographic consequences involved. The impact of man on his fellow living-beings has led Vernadsky (1945) to think in terms of a new, man-controlled period or "sphere."

On the geographical scale, one of man's agents, *fire* is of especial importance. Of course, it occurs without benefit of human interference, as a regular part of the

cycle in many places [17] but it is more often the result of man's more or less intentional act. It causes a more or less complete destruction of the climax type and a subsequent more or less elaborate recapitulation of succession. When it destroys the soil (and it will destroy organic soils!) the set-back may be a severe one, as on the irregular, polished granite and gneiss crags of the Laurentian shield with their very thin soil.

Also the mere breaking up of the continuity of certain communities can be genetically harmful, even in the case of climax associations. There is reason to suspect that such is the case of the kauri (*Agathis australis*) forest of Northern New Zealand.

Time

The *time* dimension also should be considered, both with respect to man's interference and in connection with climatic cycles, soil maturation, and the rate of plant succession.

The various scales involved in the processes outlined above have often made them very difficult to observe and even more to record. I have attempted elsewhere [18] to estimate the meaning and gravity of this situation. (See also above, under dynamics.)

Interrelations and Analogies of Vegetation Processes

Such are the criteria essential to the accurate description of vegetation. It will hardly be hoped that they can all receive equal attention, as information is rarely available on all these points, and the less so the larger the area involved. One may, however, demand consistency, If a given set of criteria be referred to, let there be no shift in emphasis in the course of application. For instance, if an author sets out to circumscribe climax areas, he should not plot locally prevalent subclimaxes on an equal basis. There should be a visible hierarchy.

Inevitably also must appear the interdependance of the different criteria cited above. Differences in stress will lead to different and even conflicting classifications and areal delimitations. For instance, the Canadian taïga or sub-arctic zone, with its open stands of scattered or bunched trees and shrubby undergrowth, harbours no major ecologically prominent species which does not appear in the more southern, tall, dense Canadian forest area whether in forest, bog or field. Environmental conditions of light, moisture, evaporation notwithstanding, the composition is fairly similar. But if *structure* be emphasized and the total physiognomy of these regions compared, the contrast is such that the southern area pertains to a forest biochore, whereas the taïga is a savana. Hare (1950) has shown that the climatic conditions are also very different.

Also, rather striking will be physiognomic similarities resulting from more or less equivalent processes. One of the most significant is the fundamental equivalence in structure between certain seres and cliseres * (Dansereau 1949a). Figure

[17] For instance in the Canadian forest. In the Province of Quebec, in 1947, 19.3% of burned areas were inflamed by lightning. (Québec, Ministère des Terres et Forêts. 1949.)

[18] Unpublished, *loc. cit.*, (b).

* Editor's note (inserted with the author's permission). The author here is trying to convey the idea of *differences* in vegetation encountered in *different places* on the earth's surface and owing their differences to differences in latitude. This use of the term *clisere* conveys neither the sense implied originally by Clements nor that inherent in the standard use of *sere* today; I believe it to be an undesirable extension of the sere concept which can create great confusion in ecological thought. In order to gain stability in ecological terminology we must take care to use special terms consistently in a given sense. If we do not, we will confuse and restrict our audience. The sere concept must be restricted to the developmental (successional) sense, implying *change* in a community in a *given place*. According to Clements ("Plant succession: an analysis of the development of vegetation," Carnegie Inst. Wash. Pub. 242. 1916, p. 347), "The clisere is the series of climax formations or zones which follow each other in a particular climatic region in consequence of a distinct change of climate." D. B. Lawrence.

FIG. 7. Four stages in succession in the St. Lawrence Valley. **A.** An invasion of bare ground by *Oenothera victorini*, with *Danthonia spicata, Solidago graminifolia.* **B.** The goldenrod association with *Solidago canadensis, S. rugosa, Festuca rubra; Poa pratensis, Trifolium repens; Polytrichum commune; Spiraea tomentosa; Prunus virginiana.* **C.** The hawthorn period, with *Crataegus* sp., *Prunus virginiana; Betula populifolia; Solidago canadensis, Festuca rubra, Spiraea tomentosa; Polytrichum commune; Pyrola elliptica, Trifolium repens.* **D.** The beech-maple climax, with *Acer saccharophorum, Fagus grandifolia; Acer pennsylvanicum, Sambucus pubens, Cornus alternifolia; Hepatica acutiloba, Viola pennsylvanica, Trillium erectum, Mitella diphylla.* For comparison with the new system, see figure 13.

7 shows four important stages in the evolution of vegetation in the St. Lawrence Valley.[19] Bare ground (sand) is at first invaded by scattered plants, such as *Oenothera victorinii, Danthonia spicata, Solidago graminifolia.* Eventually a continuous sod is formed, more or less tall grasses and forbs (*Festuca rubra, Solidago canadensis*), and even a few woody plants (*Spiraea tomentosa, Salix* spp.) extend over it. A further step involves scattered, tall shrubs (*Corylus cornuta, Prunus virginiana*) or small trees (*Crataegus* spp.) over a layer of *Solidago* and grasses. When the climax is finally reached, the stratification is much more differentiated and comprises tall trees (*Acer saccharophorum, Fagus grandifolia*), small trees (*Ostrya virginiana, Acer pennsylvanicum*), shrubs (*Cornus alternifolia, Sambucus pubens*), herbs (*Viola pensylvanica, Hepatica acutiloba, Mitella diphylla, Trillium grandiflorum*). A comparison between figures 2 and 7 would suggest that structurally the *Oenothera* stage resembles a desert, the *Solidago* stage a grassland, the *Crataegus* stage a savana.[20] The *Acer-Fagus* stage is, of course truly a forest.

A System Based on Structure

It is my purpose to present, at this point, a system based predominantly on structure, and therefore largely applicable without necessary knowledge of the taxonomic identity of the plants composing the communities.[21] I would also emphasize the fact that no causal factors need be considered, such as particular edaphic or climatic conditions or any of the processes outlined above. My principal objective is to devise a means of *recording* and *plotting* vegetation. It will serve to define stands and eventually whole plant associations and can be applied in mapping on various scales. It is implied that for small-scale purposes the dominating association will be used as an indicator and its dynamic status clearly defined. Various degrees of simplification remain possible according to the purposes at hand. From the assemblage of large numbers of formulae and diagrams obtainable by this system, it is hoped that climatic and other relationships discussed above can be deduced or at least more sharply focused. I shall attempt to illustrate some correlations which this system is likely to bring out. Several applications will be offered in order to demonstrate the method and to test the significance of the phenomena it allows to circumscribe. However, the application of this system need not imply anything more than an objective record.

Table VI shows the alternatives in each of six sets of characteristics which are considered in accordance with the principles outlined above. The significance of each will be briefly discussed.

1. Life-form

The first series concerns *life-form* and recognizes trees, shrubs, herbs, bryoids, epiphytes and lianas. Trees, shrubs and herbs are understood in the conventional sense. Examples of trees are *Acer saccharophorum, Ulmus campestris, Bertholletia excelsa, Spathodea campanulata, Mangifera indica.* Examples of shrubs: *Corylus cornuta, Cornus mas, Rhododendron ponticum, Byrsonima sericea, Arctostaphylos mariposa.* However, young trees will pass as shrubs, according to their size-class, since the space they occupy, not the transgressiveness of their growth, is being plotted. Examples of herbs: *Solidago canadensis, Oxalis acetosella, Begonia socotrana, Pennisetum purpureum, Paepalanthus polyanthos.* The category called "bryoids" includes mosses

[19] This and other successions have been described elsewhere in more detail (Dansereau 1946b).

[20] This latter analogy was pointed out by Marie-Victorin (1938) who illustrated it, see his figures 7 and 9.

[21] I would again point out that taxonomic identification of species and even infraspecific units is extremely important and will be found necessary by many workers whose requirements are only *partly* satisfied by the present method.

TABLE VI. *The six categories of criteria to be applied to a structural description of vegetation types, according to a new system (see text and fig. 8 for details)*

1. LIFE-FORM

T		trees
F		shrubs
H		herbs
M		bryoids
E		epiphytes
L		lianas

2. SIZE

t	tall	(T: minimum 25 m)
		(F: 2-8 m)
		(H: minimum 2m)
m	medium	(T: 10-25 m)
		(F, H: 0.5-2 m)
		(M: minimum 10 cm)
l	low	(T: 8-10 m)
		(F,H: maximum 50 cm)
		(M: maximum 10 cm)

3. FUNCTION

d		deciduous
s		semideciduous
e		evergreen
j		evergreen-succulent; or evergreen-leafless

4. LEAF SHAPE and SIZE

n		needle or spine
g		graminoid
a		medium or small
h		broad
v		compound
q		thalloid

5. LEAF TEXTURE

f		filmy
z		membranous
x		sclerophyll
k		succulent;or fungoid

6. COVERAGE

b	barren or very sparse
i	discontinuous
p	in tufts or groups
c	continuous

and liverworts, but also some algae, the lichens and a few other plants with a moss-like habit, such as *Selaginella selaginoides, Cassiope hypnoides, Raoulia australis.* Epiphytes are of many sorts, from the enormous tropical *Aechmaea* and *Billbergia* species to the tiny mosses, ferns, orchids and lichens. Lianas are climbing or decumbent plants, such as *Celastrus scandens, Rhipogonum scandens, Pyrostegia venusta, Valeriana scandens.*

It will be seen that the life-forms of this category do not fit Raunkiaer's classification, but cut across it in many instances, Table VII shows the correspondences between the system outlined here and Braun-Blanquet's (1932) revision of the Raunkiaerean classification. I have followed the precept of Richards, Tansley

TABLE VII. *The life-forms of Raunkiaer, according to Braun-Blanquet's (1932) revision compared to the symbols used in the system outlined here. The symbols of the new system appear on table VI; those in parentheses are alternatives, as a rule less frequent than the first mentioned*

Raunkiaer-Braun-Blanquet	Symbols of new system				
	Life-form	Size	Function	Leaf-shape and size	Leaf texture
Therophytes					
Thallotherophyta	M	l	d	q	f, k
Bryotherophyta	M	l	d	n (a)	z (f, x)
Pteridotherophyta	M	l	d	a (v)	z (f, x)
Eutherophyta	H	l (m)	d	a (g, n, h, v)	z (f, x, k)
Hydrophytes					
Hydrophyta natantia	H	l	d	a (g, n, h, v, q)	z (f, x)
Hydrophyta adnata	M	l	d	q (a)	f (z)
Hydrophyta radicantia	H	l (m)	d (e)	g (n, a, h, v, q)	z (f, x)
Geophytes					
Geophyta mycetosa	M	l	d	q	k
Geophyta parasitica	H	l	d	h (a, q)	k
Eugeophyta	H	l	e	a (g, n, h, v)	z (f, x, k)
Hemicryptophytes					
Hemicryptophyta thallosa	M	l	d (s, e)	q	f (z, k)
Hemicryptophyta radicantia	H	1 (m, t)	e	n (g, a, h, v)	f (z, x, k)
Chamaephytes					
Bryochamaephyta reptantia	M	l	e	n (v, q)	f (z, x)
Chamaephyta lichenosa	M	l	e	q	z (x, k)
Chamaephyta reptantia	H	l	d (s, e)	n (g, a, h, v)	z (f, x, k)
Chamaephyta succulenta	H	l	d (s, e, j)	n (a, h)	k
Chamaephyta pulvinata	M	l	d (s, e)	a (n, v)	x (z, k)
Chamaephyta sphagnoidea	M	m	e (s)	n (a, v)	f (z)
Chamaephyta graminidea	H	m (t)	d (s, e)	g	x
Chamaephyta velantia	F	l	d (s, e)	n (g, a, h, v)	z (x, k)
Chamaephyta suffrutescentia	F	1 (m)	e (s, e, j)	n (a, h, g, v)	z (x, k)
Phanerophytes					
Nanophanerophyta	F	l (m)	d (s, e, j)	n (g, a, h, v)	f (z, x, k)
Macrophanerophyta	T	t (m, l)	e (s, e)	n (g, a, h, v)	z (x, k)
Phanerophyta succulenta	T (F)	t (m, l)	e (d, s, j)	n (a)	k
Phanerophyta herbacea	H	t	s (d, e)	h (a, g, v)	z (z, x, k)
Phanerophyta scandentia	L	t (m, l)	e (s, e)	a (h, v)	z (x, k)
Epiphytes					
Epiphyta arboricola	E	t (m, l)	e	n (g, z, h, v, q)	f (z, x, k)

and Watt (1940): "It is . . . desirable in the first instance to keep what may be called *life-form composition* separate from *floristic composition.*" It will certainly appear to some that this principle has been carried too far in the case of the bryoids, because important physiological differences as well as taxonomic divergences are ignored. To which I would reply that in the present system, space relationships are emphasized, and the major units are physiognomical rather than biological.

2. *Size*

In fact, series 1 is inseparable from series 2, which shows *size,* or vertical extension of the individuals in the community and thus sets definite spatial minima and maxima in one dimension. Figure 8 (upper line) shows how, using cross-ruled paper, series 1 and 2 are combined to show space occupied by the various life-forms. A maximum of eight squares in height and three in width being used, the relative occupation of space can be

8
7
6
5
4
3
2
1
Tt Tm Tl Ft Fm Fl Ht Hm Hl Mm Ml Et Em El Lt Lm Ll
4
3
2
1
Ftd Fts Fte Ften Fteg Ftea Fteh Ftev Ftevf Ftdhz Ftehx Ftjnx Fteak

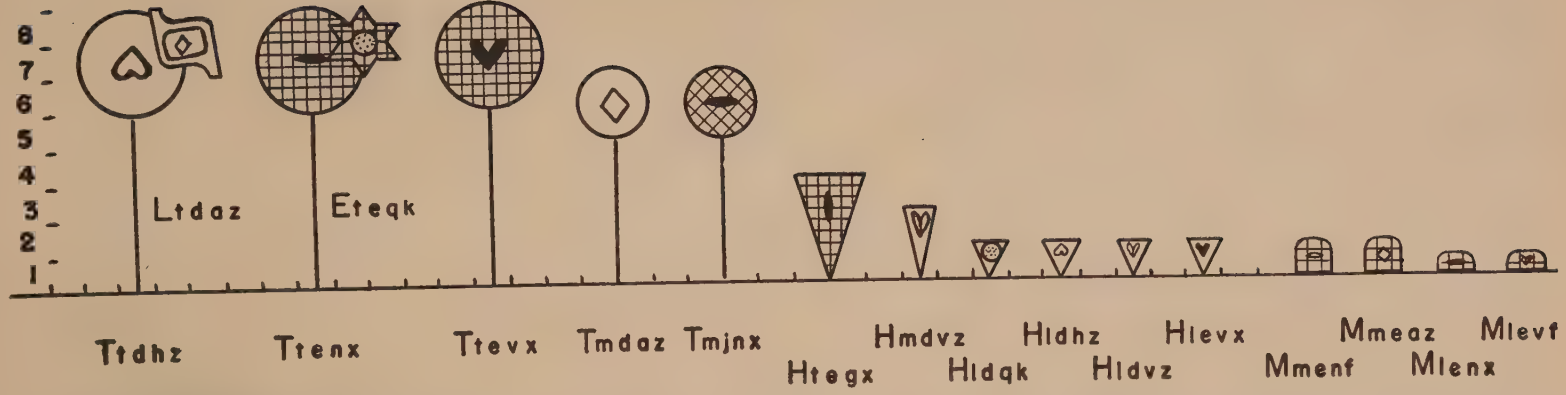


FIG. 8. Application of the symbols of table VI to several types of plants, plotted on squared paper with a maximum of eight in height and three in breadth. The upper group shows all possible combinations of series 1 (life-form) and 2 (size). The second line shows various combinations of series 3 (function) for F t (shrubs, tall); of series 4 (leaf shape and size) for F t e (shrubs, tall, evergreen); of series 5 (leaf texture) for F t (shrubs, tall). The lower line shows various applications of the five series. Each one of the formulae presented here will correspond to a large number of plant species. Suitable examples are as follows: F t e v f (*Cyathea gairdneri*), F t d h z (*Corylus cornuta*), F t e h x (*Rhododendron maximum*), F t j n x (*Cephalocereus arrabidae*), F t e a k (*Crassula arborescens*); T t d h z (*Fagus grandifolia*), L t d a z (*Celastrus scandens*), T t e n x (*Tsuga canadensis*), E t e q k (*Usnea longissima*), T t e v x (*Cabralea eichleriana*), T m d a z (*Betula populifolia*), T m j n x (*Opuntia brasiliensis*), H t e g x (*Cortaderia selloana*), H m d v z (*Desmodium grandiflorum*), H l d q k (*Amanita phalloides*), H l d h z (*Clintonia borealis*), H l d v z (*Oxalis montana*), H l e v x (*Coptis groenlandica*), M m e n f (*Sphagnum fuscum*), M m e a z (*Raoulia lutescens*), M l e n x (*Polytrichum juniperinum*), M l e v f (*Hypnum crista-castrensis*).

plotted. For herbs, the low, medium and tall categories are identical with Küchler's (1947, 1949). As for woody vegetation, the diagram of figure 9 gives a comparison of the units of the present system with both Raunkiaer (1934) and Küchler's (1949). Examples of the formulae and symbols of Figure 8 are: T t = *Liriodendron tulipifera,* T m = *Ostrya virginiana,* T l = *Betula populifolia,* F t = *Corylus cornuta,* F m = *Cornus stolonifera,* F l = *Juniperus communis* var. *depressa,* H t = *Cortaderia selloana,* H m = *Aster umbellatus,* H l = *Clintonia borealis.*

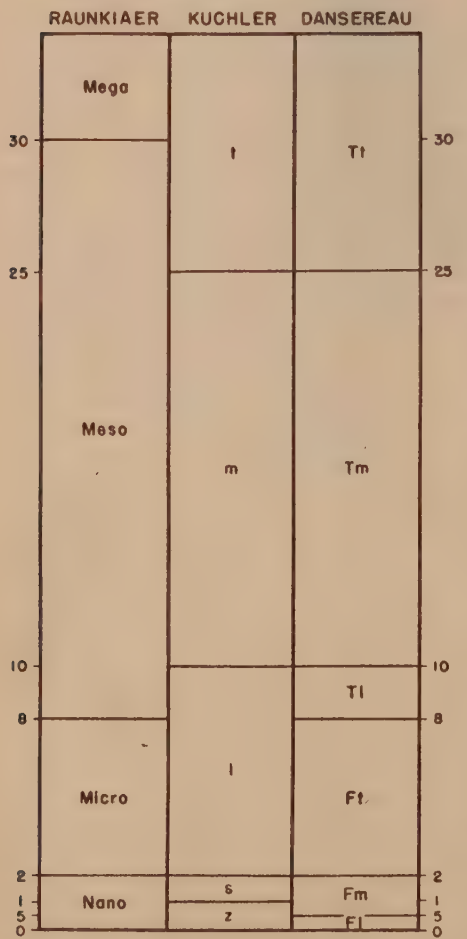


FIG. 9. A comparison of the height categories of woody plants (in meters), according to Raunkiaer (1934), Küchler (1949) and to the present system.

The plotting of bryoids, epiphytes and lianas must be on a somewhat different basis. As can be seen by a reconsideration of table VII, many taxonomic groups and several totally different types of physiological response are involved under the same spatial relationships. Bryoids will be of two kinds: the low (l) and the medium (m). Low bryoids will include loose, tufted or carpet-forming small plants of moss-like or lichenoid habit, such as *Calliergonella schreberi, Cladonia pyxidata, Selaginella selaginoides, Lycopodium inundatum, Raoulia australis.* Medium bryoids will refer to cushion-forming plants such as *Sphagnum fuscum, Raoulia lutescens.*

Epiphytes and lianas will be considered t, m or l, according to whether they rest upon a tree, shrub or herb host. Many parasites will have to be included among the epiphytes, inasmuch as occupation of space, not biological status, is being pictured here. Examples of these types are: E t = *Tillandsia usneoides* and *Psittacanthus robustus,* E m = *Usnea longissima,* E l = *Alectoria ochroleuca;* L t = *Strychnos* sp., *Bauhinia* sp., L m = *Celastrus scandens, Pyrostegia venusta,* L l = *Polygonum convolvulus, Cuscuta gronovii.*

3. Function

The third series, under the heading of *function,* concerns the periodicity of vegetative organs and the alternation of light and shade (of total space occupied at each level) in the course of a season. For instance, *Corylus cornuta* is a tall deciduous (tropophytic) shrub (F t d), *Dimorphandra mollis* is a tall semideciduous shrub (F t s), *Juniperus oxycedrus* is a tall evergreen shrub (F t e), and *Cephalocereus arrabidae* (F m j) and *Spartium junceum* (F m j), evergreens practically without leaves.

It has seemed to me very important (as it has to Küchler in his revised system of 1949) to include the last-named

category. Many woody plants of dry or semi-dry areas are more or less leafless and stand in a category by themselves: such are *Dalea spinosa, Carnegiea gigantea,* and the two species mentioned above. No less significant, I believe, is the semi-deciduous. Some communities will contain both deciduous and evergreen members; but others will consist of or contain plants that lose some of their leaves during the dry or cold period, but never all of their leaves at any one time. The tropical savana trees are often of this type as are many bog shrubs in the cold areas. All four groups are shown in figure 8: a white background shows deciduousness, a vertically striped one semi-deciduousness, a vertical-horizontal check evergreenness, and a diagonal check an evergreen-succulent or evergreen-leafless state.

4. Leaf shape and size

The fourth series superimposes *leaf shape* and *size* on the preceding. A very extensive range could be devised here in order to encompass the tremendous variations of leaves (and other vegetative organs). However, for the purpose of segregating structural units, seven broad categories are proposed: needle, scale or spine leaves (n) as in *Juniperus oxycedrus, Thuja occidentalis, Opuntia vulgaris;* graminoid leaves (g) as in *Dasylirion graminifolium, Festuca elatior, Tillandsia usneoides, Scirpus atrovirens;* medium or small leaves (a) as in *Ilex opaca, Solidago canadensis;* broad leaves (h) as in *Rhododendron maximum, Liriodendron tulipifera;* compound leaves, (v) as in *Roupala heterophylla, Dennstaedtia punctilobula;* thalloid vegetative parts (q) as in masses of algae, in fungi, and liverworts. It hardly seems desirable to indicate differences between needle (n), medium (a) and broad (h) leaves by an actual measurement of surface. So as to situate their relative order of magnitude, however, let us refer to Raunkiaer's (1934: fig. 139) classification, and say that our "needle" also include his leptophylls and nanophylls, our "medium or small" include his microphylls and mesophylls, whereas our "broad" refer to his macrophylls and megaphylls. It may appear advisable, in the course of the application of this system to recognize Raunkiaer's megaphylls as distinct from macrophylls. It might also be well to set up the leptophylls (and possibly the nanophylls too) in a separate category. Richards, Tansley and Watt (1940) used Raunkiaer's categories directly. In the case of compound leaves, they assigned the single leaflet to its size class although the measurement of the whole leaf was included in the record also. It would be quite consistent with the present system to proceed in that way and practically to disregard category v.

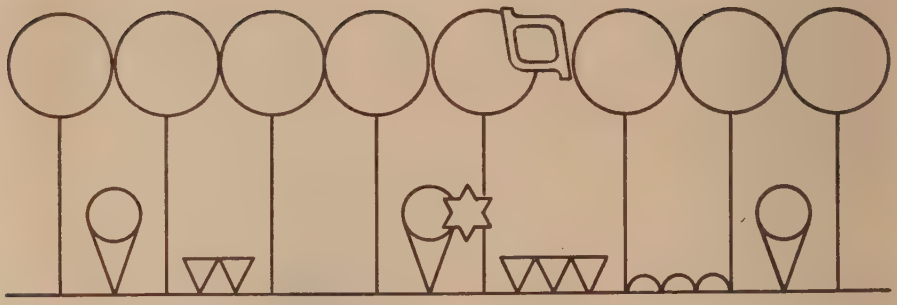
Leaf outline is not considered here, nor is leaf serration, although these characters are of considerable significance as has been pointed out by many authors, especially Bews (1927). It is felt that, together with many factors mentioned above, this feature is not relevant to the present purpose.

5. Leaf texture

Next comes *leaf texture,* of which there are four principal types: filmy (f) as in many ferns and mosses (*Hymenophyllum rarum, Adiantum pedatum, Mnium cuspidatum*); membranous (z) as in the bulk of flowering plants (*Corylus cornuta, Aster novae-angliae*); sclerophyll (x) as in many woody species (*Rhododendron maximum, Ilex opaca, Picea pungens*); succulent or fungoid (k) as in many spermatophytes and thallophytes (*Othonna crassifolia, Iresine portulacoides, Marchantia* spp., *Clavaria* spp.).[22]

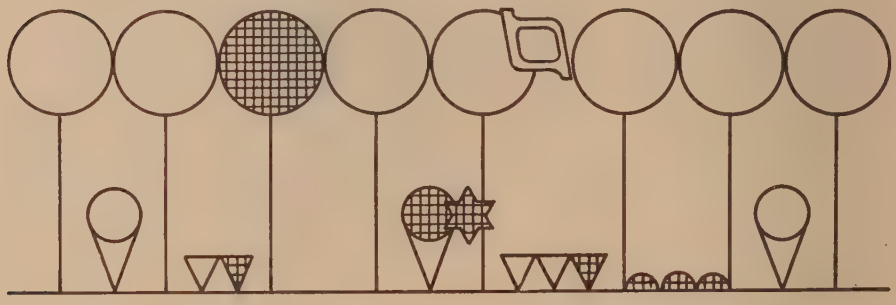
In order to apply the system now being outlined, it is necessary to grade the plant life of a community in respect to all five series of characters mentioned above. Figure 8 demonstrates various combinations of these in both algebraic and diagrammatic form. The upper line shows

[22] In some cases, the organ referred to is of course not really a "leaf."



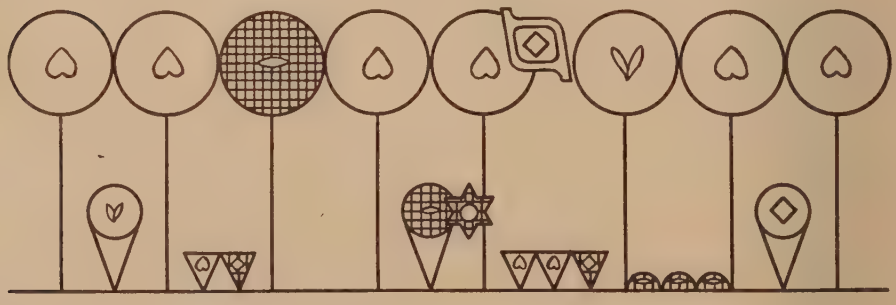
Ttc.Ltb.Fmi.Emb.Hlp.Mlp.

A Life-form and size.



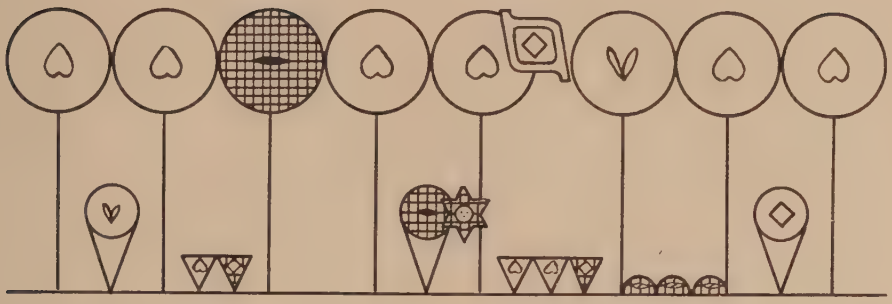
Ttdc(eb).Ltdb.Fmd(e)i.Emeb.Hld(e)p.Mlep.

B Life-form, size and function.



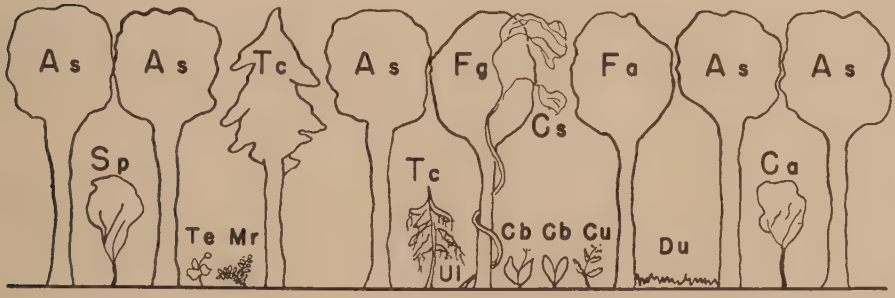
Ttdh(v)c(enb).Ltdab.Fmda(v)(en)i.Emeqb.
Hldh(ea)p.Mlenp.

C Life-form, size, function and leaf type.



Ttdh(v)zc(enxb). Ltdazb. Fmda(v)z(enx)i.
Emeqkb. Hldhz(eax)p. Mlenfp.

D Life-form, size, function, leaf type and texture.



E Semi-realistic outline of an

ACERETUM SACCHAROPHORI TSUGOSUM

Fig. 10. An illustration of the building-up and different uses of the system outlined here. The bottom line (E) is a realistic picture of a stand of *Acer saccharophorum* (A s) with some admixture of *Tsuga canadensis* (T c), *Fraxinus americana* (F a) and *Fagus grandifolia* (F g). On the beech grows a liana, *Celastrus scandens* (C s). The shrub layer consists of *Sambucus pubens* (S p), young *Tsuga* (T c), and *Cornus alternifolia* (C a). *Usnea longissima* (U l) is an epiphyte on hemlock. The herbs are *Trillium erectum* (T e), *Mitchella repens* (M r), *Clintonia borealis* (C b), *Chimaphila umbellata* (C u). The moss is *Dicranum undulatum* (D u). In the four diagrams above, the factors of series 6 (coverage) in table VI are used in combination first in **A** with series 1 (life-form) and 2 (size), then in **B** with 1, 2, and 3 (function), then in **C** with 1, 2, 3 and 4 (leaf shape and size), and finally in **D** with 1, 2, 3, 4 and 5 (leaf texture).

the combination of the first two series: life-form and size. The centre line shows a progressive building-up of the five first series as exemplified by diverse types of tall shrubs. The lower line samples a variety of plants, showing several combinations. For instance, Ftdhz and the corresponding figure represent *Corylus cornuta,* could also represent *Asimina triloba,* whereas *Prunus virginiana, Cornus alternifolia* would have Ftdaz as a formula.

6. Coverage

The sixth series consists of an arrangement of the above-mentioned formulae and symbols so as to show the *coverage of each physiognomic type.* Figure 8 has shown how each of these is built up on squared paper, a maximum of eight squares in height and three in width being used for tall trees (Tt), a minimum of one-half square in height and one square in width for low bryoids (Ml). Now, using 8 squares in height and 25 in width, the whole stand may be represented and will show the approximate percentage of cover of each one of the physiognomic types in each synusia.

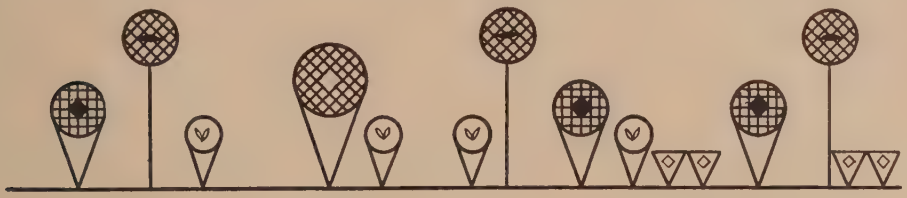
Let us take the example shown in figure 10. The lowermost diagram (fig. 10E) is a semi-realistic representation of an *Aceretum saccharophori tsugosum* (see Dansereau 1946b), a beech-maple forest containing a small percentage of hemlock. Here it appears that four layers (or synusiae) are present: a tree layer, a shrub layer, an herb layer and a moss layer. The tree layer contains *Acer saccharophorum, Fagus grandifolia, Fraxinus americana,* and *Tsuga canadensis;* also a liana, *Celastrus scandens.* This tree layer is continuous. It can therefore be represented, as in figure 10A by the formula Ttc. The liana is an isolated, infrequent feature and shows as Ltb. The shrub layer contains *Sambucus pubens, Tsuga canadensis* and *Cornus alternifolia* and the epiphytic *Usnea longissima;* it is discontinuous and shows as Fmi, Emb. The same procedure applied to the herbs (*Trillium erectum, Mitchella repens, Clintonia borealis* and *Chimaphila umbellata*) gives Hlp. And the patch of *Dicranum undulatum* shows as Mlp. It will be noted that the formulae representing the synusiae are separated by a period. Thus, we have plotted, in figure 10A, life-forms, size and coverage and stratification. For some purposes this may be all that is required.

If one cares to add function (the third series of table VI) figure 10B can be constructed. It will be noted that some symbols appear in parentheses, indicating an alternative or secondary feature. Thus, the continuous tree layer is almost entirely deciduous (d), but contains rare (b) evergreens (e), and has the formula Ttdc(eb). If one adds both function and leaf-type, figure 10C will result. When only life-form, size and coverage were considered (as above in fig. 10A), a whole synusia could be figured in a single homogeneous formula. Not so when the species involved differ in any of the last four categories of table VI. (They cannot differ in the first two, otherwise they would not appear in the same synusia.) In the example given in figure 10E, *Acer saccharophorum* and *Fagus grandifolia* both are represented by the formula Ttdhz, whereas *Fraxinus americana* is Ttdvz; these three species together form an essentially continuous canopy, occupy about 84% of the upper stratum, as each T occupies 3 squares, $7 \times T = 21$ out of 25 squares, or 84%. The corresponding formula will be, as written in on figure 10C: Ttdh(v)c. On the other hand, that layer also contains *Tsuga canadensis,* which is a tall tree (Tt) but not deciduous (d), not broadleaved (h) and not continuous (c); the hemlock is Ttenb. Therefore, the complete formula for the tree layer will be Ttdh(v)c(enb) which means: "tall trees, deciduous, broadleaved (occasionally compound-leaved), in a continuous stratum (with evergreen, needle-leaved, very scarce)."

When, as in figure 10D, leaf texture is also included, the alternations or minor features are likewise shown in parentheses. These are inserted in the formula *at the point of divergence* from the dominant type.

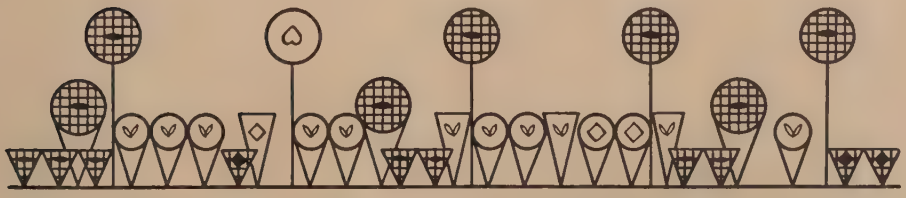
The formulae thus aligned will probably appear cumbersome and unduly complicated. They will hardly appeal to those who have not sought some kind of shorthand for their field notes and for the standardization of data taken from different sources. I can make no apology for this. I think, on the one hand, that the categories devised in table VI will seem to many biologists to provide insufficiently for variation in nature, for instance of leaf shape and size (which see above), although it is possible to subdivide and even to add to the present categories. On the other hand, I would refer those who would not be bothered with all six sets of criteria to figure 10 which shows the use that can be made of some of them without reference to the others.

As for the diagrammatic representation, it must be pointed out that the space occupied by the symbols in the diagram is not strictly to scale and that this



CARNEGIETUM FOUQUIEROSUM

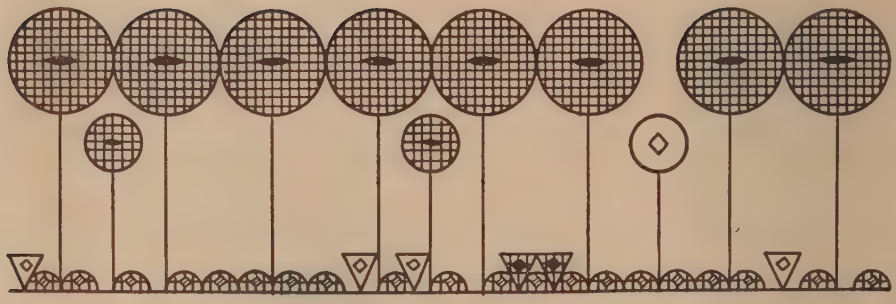
T1jnx1. Ftjazb. Fmeax1. Fldvz1. Hldazp.



PINETUM BANKSIANAE

T1enx1(dhzb). Fmenx1. Fldv(a)zp. Hmdv(a)zb. Hlen(a)xp.

FIG. 11. The sahuaro desert and jack pine barren of figure 3 plotted according to the system outlined here. It will be noted, here as in figure 10, that individual symbols do not necessarily represent individual plants. Fuller explanation in text, page 215.



PICEETUM MARIANAE

Ttenxc Tlenx(daz)1. Hldazb(eaxp). Mleafc.

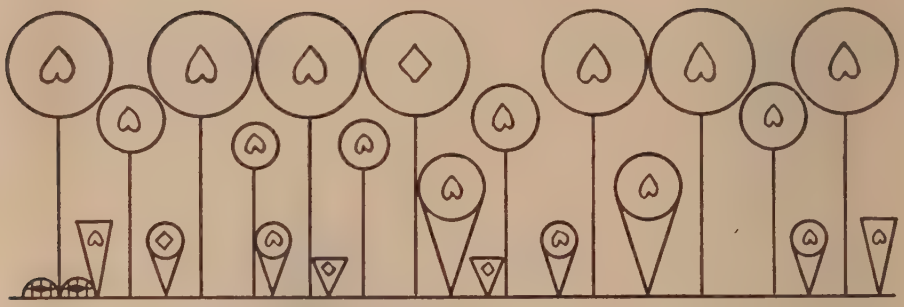
PICEETUM ERICACEUM

Tl(Ft,Fm)enxi. Flsaxp. Mm(l)eafc.

CHAMAEDAPHNETUM
CALYCULATAE

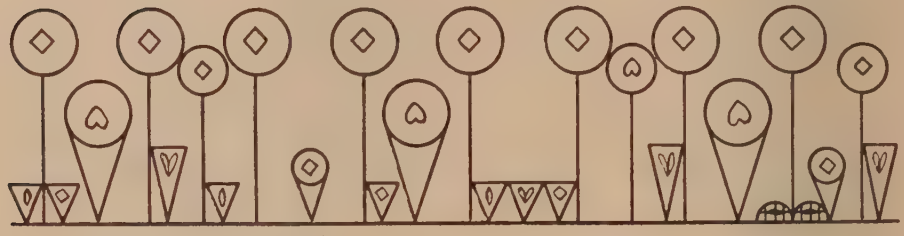
Fmenxb. Flsaxc. Mmeafc. Mleafp.

FIG. 12. A bog sere on the Laurentian Plateau, from the unistratal tall sedge association bordering open water to the Canadian forest climax.



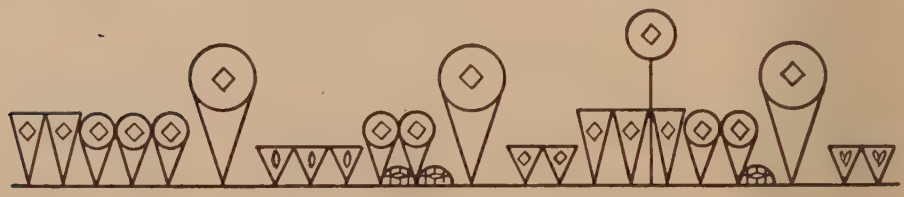
ACERETUM RUBRI

Ttdhzc(azb). Tmdhzi. Tldhzp. Ftdhzi.
Fldhzi(azb)-Hmdhzb. Hldazb. Mlenxp.



BETULETUM POPULIFOLIAE

Tmdazi. Tlda(h)zb. Ftdhzb. Fldazb-Hmdvb.
Hldg(a,v)p. Mlenxp.



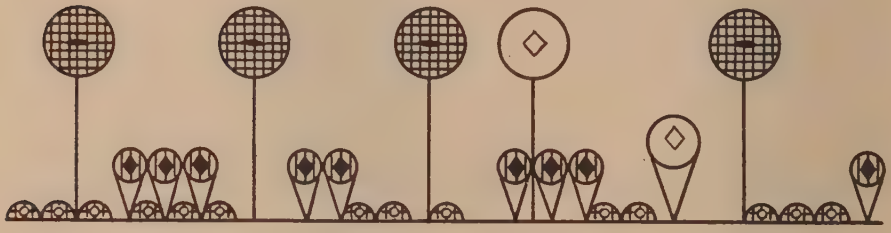
CRATAEGETUM BOREALE

Tldazb. Ftdazi. Fl(Hm)dazp. Hldg(a,v)zp. Mlenzb.

FIG. 13. A group of six associations characteristic of a segment of the xerosere in the St. Lawrence Valley, showing the differences in structure from early pioneer stages to a subclimax, as brought out by the present system of illustration. This had already been partly drawn in figure 7. The diagram for the climax *Aceretum saccharophori* is given in figure 14.

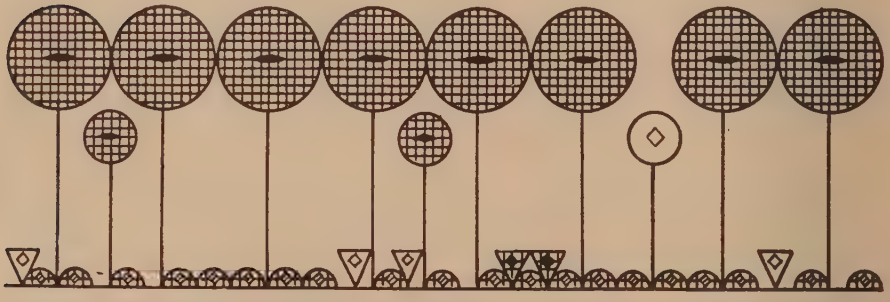
VACCINIETUM ALPINI

Fidazp.Hidgzb.Mieqzp.



PICEETUM HUDSONIANUM

Tmenxi(dazb) Fmdazb.Fisaxp.Mieqzp



PICEETUM MARIANAE

Trenxc.Tlenx(daz)i.Hidazb(eaxp).Mieafc.

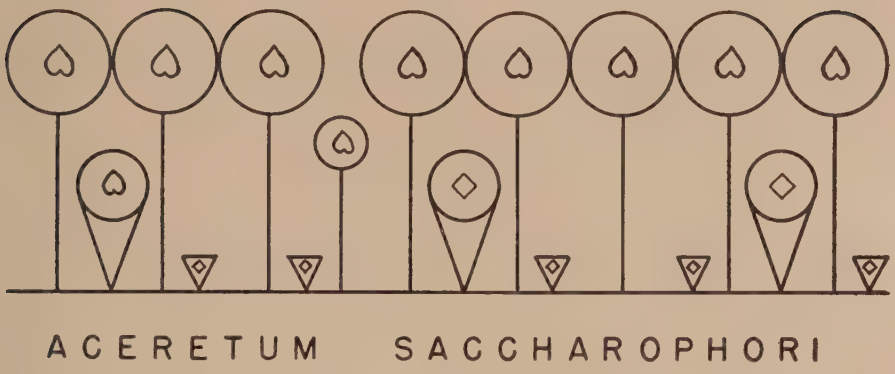


FIG. 14. The climax plant community in four climatic zones along a transect running roughly from parallels 45° to 60° lat. N in Quebec Province, or from sea level to 4,000 feet in the Gaspé Peninsula (see Dansereau 1946a: fig. 2). Structure of the arctic heath, the park-like taiga, the Canadian coniferous forest and the deciduous forest are in strong contrast.

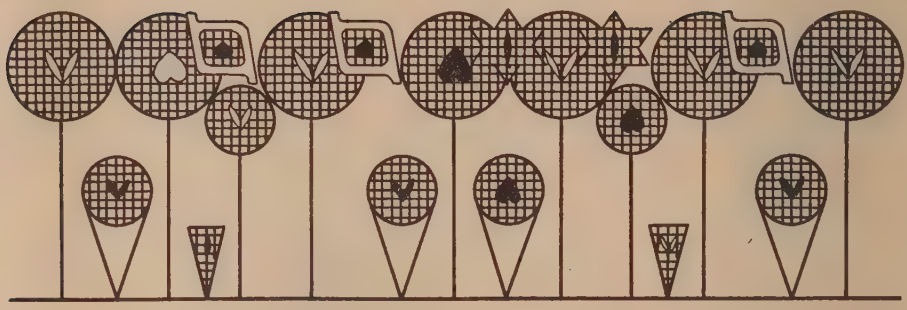
means of representing vegetation is only partly pictorial. It must also be noted that each individual symbol stands for the relative amount of space occupied in its synusia by the type of plant it represents. A look at figures 3 and 11 on the one hand and 7 and 12 on the other hand, will show that one symbol may stand: a) for several individuals of a species; b) for individuals of several species all of which are referable to a single type in terms of the present classification. These diagrams have the merit of showing at a glance differences and similitudes of many kinds. A few applications of the system will serve to further illustrate this point.

SOME APPLICATIONS OF THE NEW SYSTEM

As has been stated above, plant communities may be approached and recorded with the aid of the system outlined here. There are many methods of studying vegetation, and synecological studies have proceeded along widely different lines. Because of this, the present proposal will have a very different appeal and value for different schools, and also according to whether one considers its application to field work, to the compilation of data or to mapping.

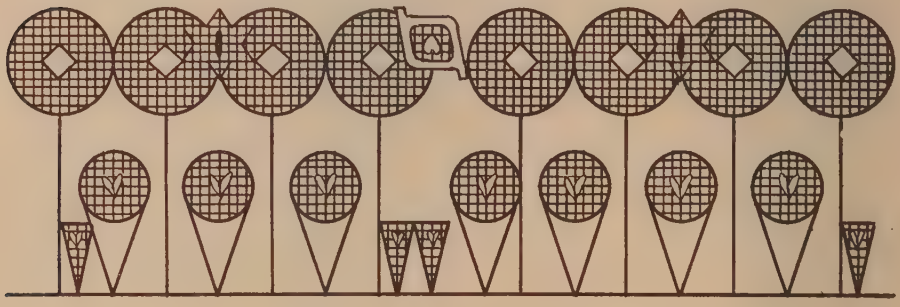
Many ecologists have published semi-diagrammatic transects of vegetation, to show relation to topography (for instance, Dachnowsky-Stokes (1912), Richards, Tansley, and Watt (1940), Transeau, Sampson and Tiffany (1940), Hough and Forbes (1943), Beard (1944), Dansereau (1943, 1946, 1947), Egler (1948)). These more or less realistic drawings can be compared with figures 2, 3, 7 and 10E as to general style. They cannot be too well compared with one another and certainly do not show the same number of factors that are encompassed in the system proposed here.

Figure 12 is a field record which can be compared with Dachnowsky-Stokes' (1912) well-known diagram. It illustrates various stages in succession (also contiguous in zonation) in a typical bog sere on the Laurentian Plateau. Reading from the bottom upwards, the changes in structure can be readily followed: the graminoid, open, tall sedge meadow of *Carex rostrata* (Hmdgxc) contains a few individuals of *Myrica gale* (Fldazb). At the following stage, *Myrica* becomes dominant (Fldazp) through spreading in



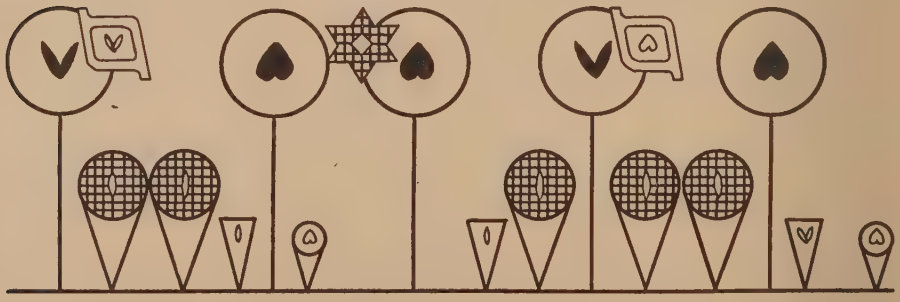
LECYTHIDETUM AMAZONENSE

Tteh(v)z(x)c. Ltehxl. Etegxp. Tmeh(v)z(x)b.
Ftev(h)xi. Hmegx(vz)b.



CERATOPETALETUM
AUSTRALIENSE

Tteazc. Ltehzb. Etegxi. Ftevzc. Hmevzb.



TECTONETUM GRANDIS

Ttdh(v)xi. Ltdv(h)zi. Eteazb. Ftegzp. Fldhzb.
Hmdg(v)zb.

patches; some *Carex rostrata* persists (Hmdgxi) and some *Carex disperma* (Hldgzb) appears, together with a little *Sphagnum* (Mleafb). The third stage shows a well-developed *Chamaedaphne calyculata* layer (Flsaxc) with a solid undergrowth of *Sphagnum* (Mmeafc); black spruce, *Picea mariana* (Fmenxb), has appeared and also a few patches of *Calliergonella schreberi* (Mleafp). In the fourth stage, *Chamaedaphne* (Flsaxp) has become quite patchy, as spruces of various sizes now occur (Tl(Ft,Fm) enxi); *Sphagnum,* however, is still essentially continuous, but now alternates with broader patches of *Calliergonella.* The final sketch shows the climax association, the spruce forest with its canopy of coniferous trees (Ttenxc), its thin layer of the same conifers plus a few alders or hazels (Tlenx(daz)i); the herb stratum is also rather scattered with *Clintonia borealis* (Hldazb) and *Linnaea borealis* (Hleaxp); the mosses (*Calliergonella schreberi* and *Hypnum cristacastrensis*) form a dense carpet (Mleafc).

Figure 13, likewise directly drawn from field observations, shows another successional group, this time from a xerosere leading to the deciduous forest climax in the Montreal area, (*Aceretum saccharophori laurentianum*). The segment illustrated here has already partly been shown in figure 7. It starts with the evening-primrose association on a sand plain and leads to the red maple subclimax, further progression to the climax not being shown.[23] The details of the composition of this sere may be found elsewhere (Dansereau 1946b). Maybe the most remarkable feature illustrated here (in contrast to fig. 12) is the prevailing deciduous and small-leaved plants that play the leading rôles at every one but the last stage. The evolution of structure is, of course, quite remarkable and brings about important biological changes affecting evolutionary opportunity.[24] Thus, the geneticist will note the immediate elimination (at the second stage) of *Oenothera*; the great abundance of the highly variable *Solidago canadensis* and *S. rugosa* at the third; the almost complete elimination at that same stage of the non-indigenous species which are very numerous at the second stage; the relatively brief span of *Crataegus,* one of the most eccentric and mutable of North American genera.. It has been suggested by Cain [25] that "open" and "closed" communities offer entirely different sets of evolutionary opportunities for plants. The diagrams of figure 13 show various degrees in the gradual closing of the communities, each one being more so than the preceding.

And now, casting our attention on another scale, we have, in figure 14, a representation of the structure of the climax-association in the four principal climatic belts traversed by a transect running roughly from Montreal to Ungava Bay, that is from 45° to 60° lat. N. The same relation obtains from sea-level to 4,000 feet in the Gaspé Peninsula (see Dansereau 1946a: fig. 2). Here are four structures that appear to correspond to the ultimate point of evolution of vegetation in colder and colder climates (and probably an appreciably drier one in the case of the *Piceetum hudsonianum*). The climax, being essentially controlled by

[23] The *Aceretum saccharophori* is drawn in figure 14.

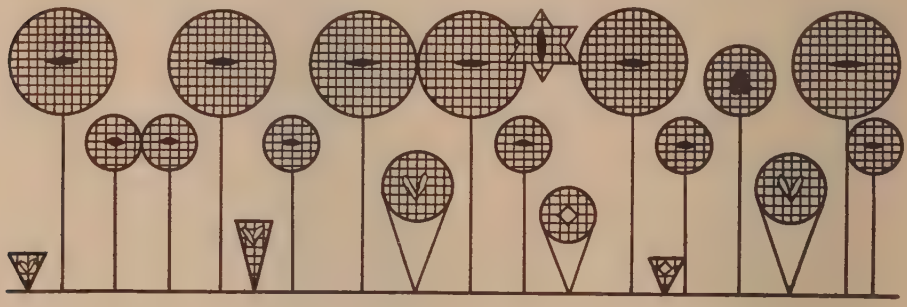
[24] Dansereau, unpublished, *loc. cit.,* (a).

[25] In an unpublished paper "Species-area relationship, closed communities and evolutionary opportunity" read at the third annual meeting of the Society for the Study of Evolution. New York, November, 1948.

FIG. 15. Schimper and von Faber's (1935) types. 1. *Tropical rainforest, Lecythidetum amazonense,* from original data collected near Manaus, Brazil. 2. Subtropical rainforest in New South Wales (*Ceratopetaletum australiense*), from the data of Brough, McLuckie and Petrie (1924). 3. Monsoon forest of Burma (*Tectonetum grandis*) according to the data of Schimper (1903).

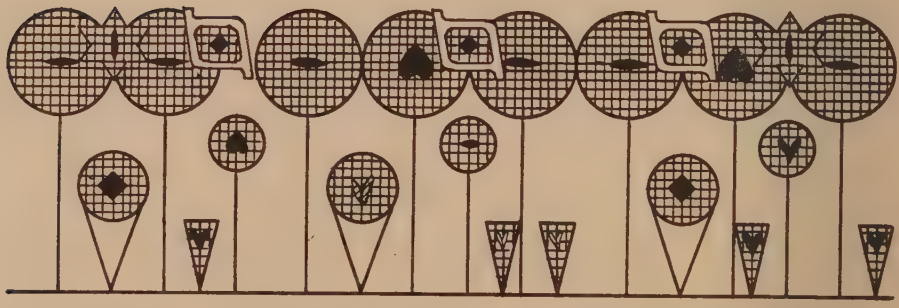
climate rather than soil or other more immediate factors, is the most reliable over-all index of conditions for life in a given area. Its structure even more than its composition cannot fail to be significant: stratification, coverage (or spacing) and leaf type occur in four different combinations and indicate a completely different final adjustment to light, heat and moisture. That is to say that the microclimate-macroclimate relationship is one which is peculiar to each zone.

Now, in the case of the two lower diagrams (*Piceetum marianae* and *Aceretum saccharophori*), figures 12 and 13 show us how such an adjustment is eventually achieved, show us in each case one of the many paths followed by succession to-



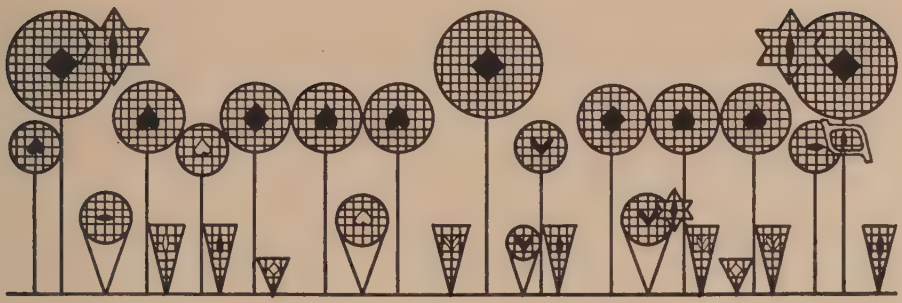
ARAUCARIETUM JORDANENSE

Ttenxc. Tmehxb. Tlenxc. Etegxb. Ftevfi. Fmeaxb. Hmevzb. Hlev(a)zb.



DACRYDIETUM CUPRESSINI

Tten(h)xc. Lteaxi. Etegxi. Tleh(n,v)xi. Fteax(vf)i. Hmevz(x)i.



AGATHIDETUM AUSTRALIS

Tteaxi,Etegxi; Tmeh(a)xc. Tleh(n,v)x(z)i. Ltegxb;
Fmen(v,h)x(z)i. Emegxb; Hmevz(gz,gx)i; Flevxb. Hleazb.

FIG. 16. The *temperate rainforest,* no. 4 of Schimper and von Faber (1935). *Araucarietum jordanense,* from original data collected at Campos do Jordão, state of São Paulo, Brazil. *Dacrydietum cupressini* from the data of Cockayne (1921) in New Zealand. *Agathidetum australis* from original data collected in Waipoua forest, North Island, New Zealand.

wards the climax. It is not without interest to look back on these diagrams and to discern some equivalence between seral and cliseral * relative positions. The arctic heath or tundra, in structure, is quite similar to the *Chamaedaphnetum* (fig. 12), while the *Piceetum ericaceum* bears some resemblance to the Hudsonian savana (*Piceetum hudsonianum*), for instance.

Turning back to figures 2 and 7, where this analogy between local succession and clisere * was first suggested, we may compare them with figures 12, 13 and 14 and see that the evolution of vegetation, whether following upon the "improvement" of *microclimate* in a single locality or of *climate* over a broad transect, follows essentially the same pattern: *an increasingly favourable combination of temperature and moisture permits increased closing, elevation and differentiation into strata of the community.* The peak of differentiation is represented by forests; this ultimate stage in cold or dry climates is variously inhibited at the savana level, at the prairie level, at the desert level.

On the still broader, world scale, figures 15–19, have been compiled (mostly from original data) to show the most striking differences between some of the principal formations as exemplified by what is presumably climax. All fifteen of Schimper and von Faber's (1935) formation-types are shown in figures 14–19. A critical review of these fifteen types themselves would certainly show that some of them are quite heterogeneous and require further subdivision, but this need not be questioned for the purposes now at hand,[26] as our diagrams show at once the differences and similarities between any two types. It is hoped that the examples used for each one are fairly typical of the formation as a whole. Actually, it has seemed interesting to show several examples in some cases so as to illustrate variation. Thus, figure 16 shows three temperate rainforests and figure 20 shows four climax types al-

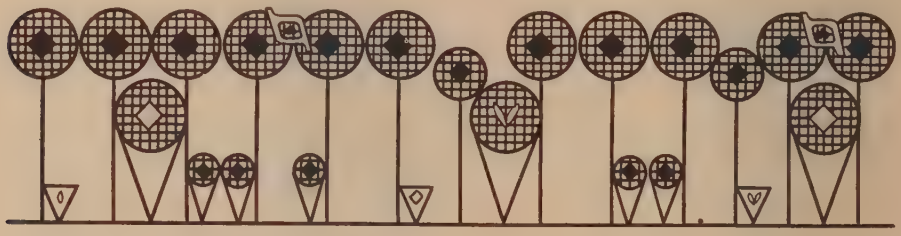
* See Editor's note, p. 197.

[26] If Schimper and von Faber's formation-types need re-casting, it may be that the present system will offer a small contribution by providing a new instrument for comparisons.

ready illustrated by other instances. It seems to me that the case of the *Nothofagetum cliffortioidis* supports the value of the present method of comparison, as it minimizes the floristic differences and casts the whole attention on structure and function. This subalpine forest is seen to resemble the Swiss subalpine spruce forest (*Piceetum montanum*) and the Canadian forest also, both of them coniferous! It is a fact that strikes most ecologists that many of the New Zealand beech stands have the physiognomy of coniferous forest.

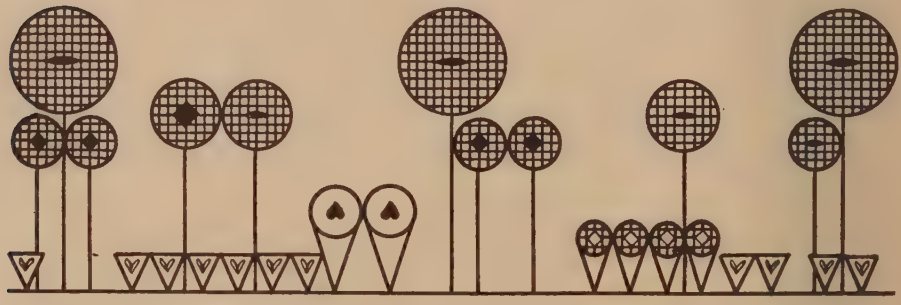
Figure 21 shows three shrub formations in three widely separated areas: California, New Zealand and southern France. The analogy is quite striking as to general structure of the communities, whereas there is some variation in leaf-type.

I have plotted many other communities, on the basis of the present system, but will not attempt further demonstration for the moment, as it would seem that the examples chosen already illustrate a rather wide range of geographic and ecological situations.



QUERCETUM ILICIS

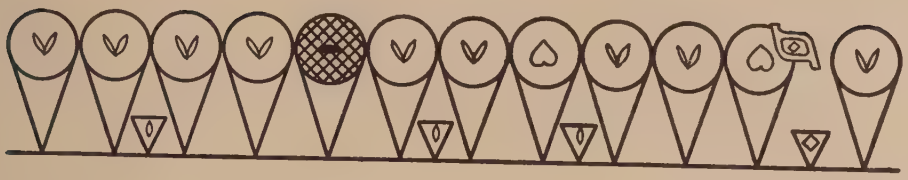
Tmeaxc. Ltea(h)xi. Tleaxb. Ftea(v)zi. Fleaxp. Hlda(v,g)zb.



PINETUM PONDEROSAE

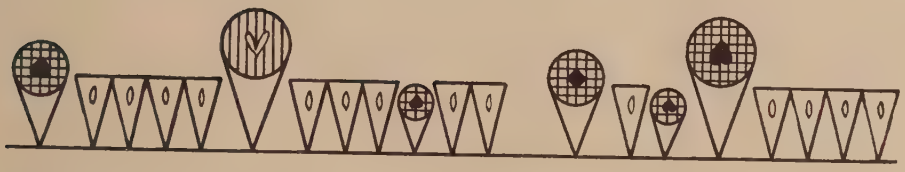
Ttenxi. Tmen(a)xl. Tlea(n)xp. Fmehxp. Fleazp. Hldvzp.

FIG. 17. Schimper and von Faber's (1935) nos. 7 and 8. The mediterranean *evergreen hardwood forest, Quercetum ilicis,* from the data of Braun-Blanquet (1936). The yellow pine *savana woodland, Pinetum ponderosae,* from data collected in the Sierra Nevada.



MIMOSETUM CAATINGAE

Ftdvzc(hzb,jnxb).Lmdazb.Hldg(a)zl.



DIMORPHANDRETUM MOLLIS

Ftsvz(ehx)b.Fmeh(a)xi.Hmdgzc.Flehxb.

ANDROPOGONETUM IOWENSE

Hmdgzb.Fldvzb.Hldg(a)zc.

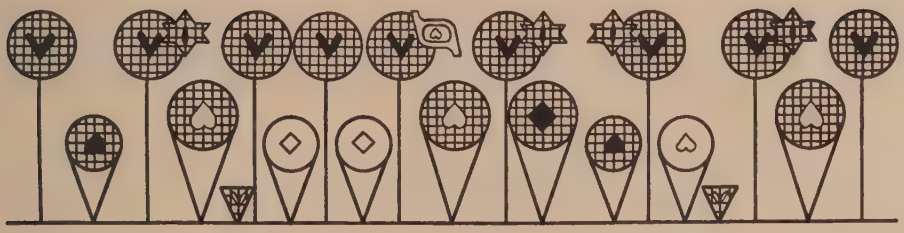
FIG. 18. Schimper and von Faber's (1935) nos. 9, 10, and 11. *Mimosetum caatingae* a *thorn scrub* observed near Fortaleza, northeastern Brazil. *Dimorphandretum mollis*, a "campo cerrado" or *savana*, at Pirassanunga, state of São Paulo, Brazil. *Andropogonetum iowense*, a prairie in western Iowa.

FIG. 19. Schimper and von Faber's nos. 12 and 13. The *heath* of Northwestern Europe (*Callunetum vulgaris*), according to Warming (1909). The dry desert (*Carnegietum giganteae*) as it appears in Southwestern Arizona.

It may prove worthwhile, at this point to review what the present system is capable of showing and what it cannot represent. The principal items, already discussed above, have been collected in table VIII.

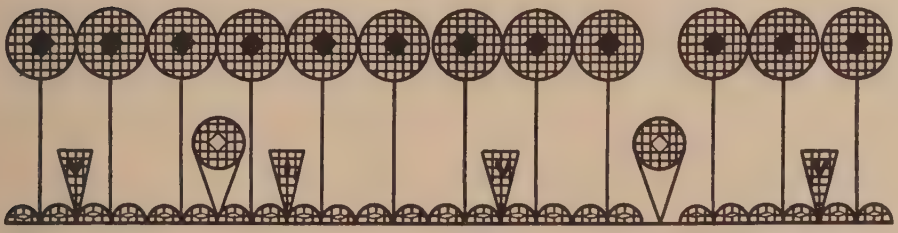
Description of vegetation is preliminary to *classification*. A uniform application of the same criteria will permit comparison. But a hierarchy of criteria is necessary for classification. Although I have suggested such a hierarchy I am not now proposing any system of classifying vegetation, although I feel that the present scheme would offer a more satisfactory framework than both Rübel's (1930), and Schimper and von Faber's (1935). I am also in doubt as to whether Küchler's *system* (1949) truly provides a *classification*. His papers (1947, 1949, 1950) offer no final discussion of the *categories* that actually materialize out of the almost indefinite number of possible combinations his scale provides for.

The merits and shortcomings of this new system will undoubtedly appear in the course of application. It is fully expected that some modifications will prove necessary, both in view of unforeseen situations and new applications and in view of some inherent defects in the conception. The author will be most grateful for criticism of all and any kind and does not wish to distinguish between the constructive and destructive as he feels that he must bear the burden of putting criti-



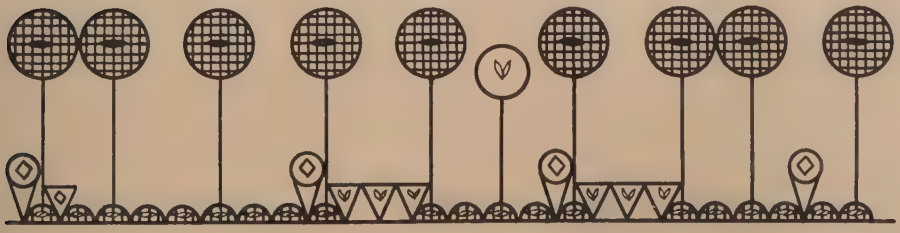
CABRALETUM MONTANUM

Tmevxc. Lmdhzb. Emegxp. Ftehz(ax)l. Fmehx(dhz,daz)l. Hlevzb.



NOTHOFAGETUM CLIFFORTIOIDIS

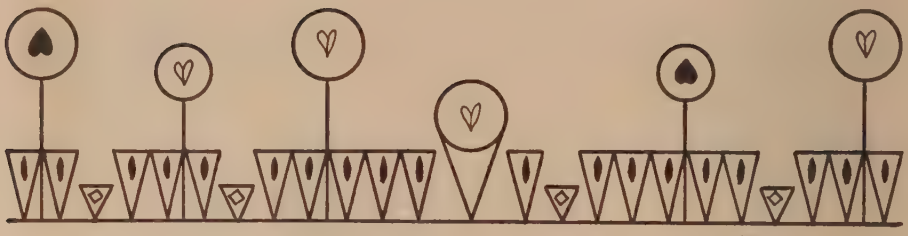
Tmeaxc. Fmeazl. Hmev(g)xi Mlenzc.



PICEETUM MONTANUM

Tmenxc. Tldvzb. Fldazi. Hldv(a)zp. Mlenfc.

FIG. 20—*Continued on next page*



ANACARDIETUM
COSTA-RICENSE

Tm (l) d v z (h x) i. Hm d g x c. Hl d a z l.

FIG. 20. Some interesting climax types for comparison with figures 14–19. *Cabraletum montanum,* a montane rainforest in Southeastern Brazil (from original data), rather close to no. 2 (as exemplified here by *Ceratopetaletum australiense,* fig. 15). *Nothofagetum cliffortioidis,* another montane type, as seen at Arthur's Pass, South Island, New Zealand, actually derived from temperate rainforest of the types shown in figure 16, but rather similar to no. 6 (as exemplified here by *Piceetum marianae,* fig. 14). *Piceetum montanum,* a subalpine forest in Arosa, Switzerland, is quite similar to *Piccetum marianae* (although more open, like *Piccetum hudsonianum*) and small, like *Nothofagetum cliffortioidis. Anacardietum costa-ricense,* the Costa Rican savana (from the data of Standley 1945) shows some resemblance to the Brazilian cerrado and caatinga (fig. 18) and also to the Arizonian desert (fig. 19), and even to the Hudsonian taiga (fig. 14).

TABLE VIII. *What the present system (of table VI) shows and does not show*

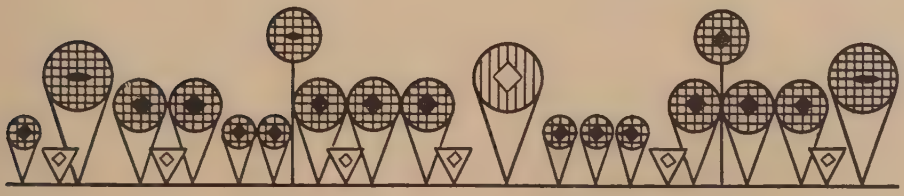
It shows:	It does not show:
1 and 2: *Life-form and Size*	
Height of vegetation in all layers	Outlines of individuals (flat-topped, cone-shaped, rounded, etc.); compare figures 3 and 11, see figure 10
Space occupied	Actual life-form (Raunkiaer)
Woodiness and herbaceousness	Branching and habit (except M, E, L)
3: *Function*	
Degree of deciduousness	Time of deciduousness, position of regenerating buds (see above under life-form)
4: *Leaf Shape and Size*	
Six classes based on size and outline	Actual shape of leaves, incision, serration, pubescence, position
5: *Leaf Texture*	
Four principal types	Actual function (xerophytic, etc.)
6: *Coverage*	
Space occupied by each type in terms of 1–5 above	Distribution and density of individuals
Relative distribution of plants in each layer	Distribution of plant masses on scale

ADENOSTOMATETUM
FASCICULATI

Fmenzc(axi).Hlda(g)zp.

LEPTOSPERMETUM SCOPARII

Fmenxc.Hldgzp(eaxb).



CISTETUM LADANIFERI

Tlen(a)xb.Ftenx(saz)l.Fmeaxp.Fleaxp.Hldazl.

FIG. 21. Three shrub formations: the Californian soft chaparral (*Adenostomatetum fasciculati*), the New Zealand manuka scrub (*Leptospermetum scoparii*), and the Mediterranean rock-rose maquis (*Cistetum ladaniferi*); all from original data.

cism to good use and improving a scheme which he has imagined can be of some value to others.

Summary

1. Various approaches to the study of vegetation are reviewed: floristic mapping, life-form statistics (table I, fig. 1) and ecological classifications (table II) especially.

2. The structural-physiognomic point of view is outlined (table III, figs. 5, 6) and Küchler's new system (table IV) is discussed as an improvement over all preceding efforts.

3. The fundamentals of the description of vegetation are considered at some length, as well as the relations of vegetation. Some interrelations and analogies of vegetation processes are emphasized, especially as they are revealed by structure.

4. A new system is proposed (table VI, figs. 8, 10) in which six series of criteria are used: 1. life-form; 2. size; 3. function; 4. leaf-shape and size; 5. leaf texture; 6. coverage. The grading of vegetation can be carried on either by formulae (letters) or diagrams.

5. Various applications of the new system are offered, showing the similarities and differences between communities of a sere (figs. 12, 13) or a clisere * (fig. 14) and communities of widely separated but more or less analogous areas (figs. 14–21).

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* See Editor's note, p. 197.

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ECOLOGICAL STUDIES OF THE BOOK LOUSE, *LIPOSCELIS DIVINATORIUS* (MÜLL.)[1]

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The book louse, *Liposcelis divinatorius* (Müller), belongs to the order Corrodentia, suborder Heterotecnomera, and family Liposcelidae (Essig 1942). The synonymy of this species (Gurney 1939) is as follows:

Liposcelis divinatorius (Müller)

Termes divinatorium Müller, Zoologiae Danica prodromus, seu animalum Daniae et Norvegiae indigenarum (1776) : 184.

Troctes divinatorius Hagen, Verh. Zoolbot. Ges. Wien 16 (1866) : 220.

Troctes fatidicus Enderlein, Zool. Exped. Egypt White Nile, 1901, 18 (1905) : 36–38.

It has been known by various common names such as book louse, mold louse, dust louse, cereal psocid, cabinet mite, and cheese mite (Hartnack 1939; Finlayson 1932), based on its superficial resemblance to a louse, nature of food and habitats. *Trogium pulsatorium* (L.) has also been referred to as book louse, but the American Association of Economic Entomologists (Anonymous 1931) has restricted the name book louse to *L. divinatorius*. It has also been called "death watch" because of a faint ticking noise associated with it in houses. Though sound production in certain species of Corrodentia has been demonstrated (Pearman 1928b), there is no definite record of this phenomenon being exhibited by the book louse. No evidence of sound production by the book louse was observed by the writers. The confusion seems to have arisen due to misidentification of the species concerned.

The book louse, though one of the smallest members of the order, is probably the most troublesome and destructive one (Essig 1942). In addition to inflicting direct damage by feeding on animal and vegetable matter, it causes great annoyance. Because of its world-wide distribution it has assumed an international importance. However it has not received much attention from the entomologists and our knowledge of this insect is meager. Little was known of the biology of the book louse until 1930 when Rosewall published the results of his studies. Since then two articles by Candura (1932) and Finlayson (1932) have given additional information.

The book louse is in most buildings but escapes notice because of its small size and concealing habits. Under favorable conditions it becomes extremely abundant. The control of this insect is difficult, tedious, and expensive, due to its retiring nature. No insecticide can give an effective control unless is reaches all cracks and crevices, interior of walls, behind loose wall paper, upholstered furniture, stuffed mattresses, and other similar places of abode.

Lack of information and the importance this insect has gained in recent years, prompted these studies. A study has been made of the biology of the book louse under a few conditions of temperature and moisture. A knowledge of the physical requirements of this insect may prove useful in creating conditions in houses unfavorable for its multiplication, and thus avoid costly methods of insecti-

[1] Presented as a portion of a Doctorate thesis at the University of Massachusetts.

cidal control. Its food requirements and habits need further investigation.

Review of Literature

The literature on the book louse, *L. divinatorius,* is rather scanty. According to Back (1939b), the Review of Applied Entomology contained, on an average for the last twenty-five years, one reference annually to psocids in supplies or crops. The Insect Pest Survey from 1921 to 1939 contains 131 references to all psocids, mostly of localities and food materials.

Economic importance

A number of species of Corrodentia frequent houses, of which *L. divinatorius* is the most common and important. It is almost omnivorous in habits, feeding on any animal or vegetable matter (Marlatt 1896; Back 1920; Back and Cotton 1930; Candura 1933). It damages books, wall paper and photographs by eating away the starchy paste and glue used in their preparation. It feeds upon and destroys entomological and zoological specimens, herbaria, upholstered furniture, and mattresses filled with husk, hair, straw or feathers, microscopic preparations, potted plants, dried fruits, ground feed, flour, cereals, and other farinaceous materials (Marlatt 1896; Pliginsky 1915; Hungerford 1924; McDaniel 1928; Candura 1933; Kemner 1933; Peus 1933; Hartnack 1939; Hawkins 1939; Garcia 1940). It is a pest of grain and there are definite instances on record of its damage. It destroyed corn stored in glass-stoppered jars at the Agricultural Experiment Station in Connecticut. The external surface of kernels was completely eaten away, rendering the variety wholly unrecognizable (Britton 1900). A wheat sample kept in glass jars was heavily infested. It ate away the germ of 35 per cent of the grains and reduced germination from 93 to 33 per cent (Cooley 1914). Samples of polished rice were destroyed and being reduced to powder in Hawaii (Pemberton 1942). It has been recorded feeding on *Sitotroga* eggs, and also chorions, if starved (Finlayson 1932).

Some workers, on the other hand, are inclined to rule out the book louse as a pest of any great economic importance. They think it feeds on molds and seldom does any real damage. Back (1939a, b, c) reported that no instance of direct injury by psocids to any material had come to his notice in the past twenty years. The cause of heavy losses to property owners is not due to destruction of buildings and furnishings, but rather to broken leases, lawsuits, and fees to pest control operators. It is seldom a pest of any importance in grain and other stored products (Chapman 1921; Back and Cotton 1930; Weiss and Carruthers 1936; Back 1939b; Shepard 1939a, b; Cotton 1941; Linsley and Michelbacher 1943).

During the course of these studies, the book louse has been observed feeding on flour, grain and other organic matter, though it would consume molds, if available. In addition to the annoyance it causes, it is a potential pest.

Rearing techniques

Rosewall (1930) placed an adult in the cell of a drop culture slide with a few grains of corn meal and covered the cell with a cover slip, held in position by a small amount of vaseline. The eggs when laid were removed by means of a needle and placed in similar separate slides. Corn meal alone, however, does not seem to be a complete food for the book louse.

Sommerman (1942) reared about ten species of Corrodentia, including *L. divinatorius,* using five different methods. The insects in all cases were reared on corn sheath having mold on it. In one case she used a glass cylinder fitted with a cork having two notches on the sides to act as air escapes and a hole in the center for the insertion of a glass tube, which was plugged with cotton. The corn sheath, along with the insects,

was placed in the cylinder. The cotton plug in the glass tubing was soaked with water once a day to maintain humidity. In the other four methods, wide glass tubes were used in place of the cylinder. These were closed at the ends, either with cotton plugs or with corks having pieces of small glass tubing plugged with cotton. The cotton plugs were either moistened directly or cotton-plugged tubing was dipped in water to act as a wick. She also attempted to rear them using one of these methods at 21.1° C. and various relative humidities, but abandoned it due to high mortality, for which no reason is offered.

The methods used by these workers were not suitable for ecological studies on the book louse, and hence were not employed.

Sheehan (1943) used small glass bottles 2 inches in height and 1.5 inches in diameter, and vials 2.5 inches in height and about 0.75 inch in diameter. The cages were not covered as the insects were unable to crawl up if the sides were kept clean. She recommended Mead's cereal, Pablum, or wheat flour for food. The food had to be changed frequently at high humidities to avoid excess fungus growth, not because it had any harmful effect on the insects, but to facilitate their handling. A crumpled piece of paper toweling was placed in the cage for egg deposition and to provide a hiding place for the adults. Most of the eggs were laid on the paper, very few in the food, and none on the side of the cage. This method, with slight modification, was used successfully in the studies reported here.

Biology

Habits and habitats. The habitat of the book louse is almost exclusively inside buildings, but in some seasons it may be found under the bark of trees (Finlayson 1932). It is met with frequently in all sorts of places in houses which are not disturbed. Any organic material stored over long periods is liable to attack. Musty unused books, upholstered furniture and stuffed mattresses provide excellent abodes for its multiplication. The insect prefers dark, damp places and its rapid multiplication occurs under humid and warm conditions. Cold weather and dryness check its abundance (McDaniel 1928; Candura 1932, 1933; Weiss and Carruthers 1936; Back 1939a, b, c; Hartnack 1939; Gibson 1940; Linsley and Michelbacher 1943).

Observations of Noland (1924) that the favorite habitat of the book louse was a dry and undisturbed place do not seem to be correct.

Life history. The adults are about 1 mm. long, and vary from light brown to grayish brown in color. They reproduce parthenogenetically, only females being known. The pre-oviposition period varied from 31 to 45 days, with an average of 45, during October to January (10° to 36° C.). At 26.7° C. and 65 per cent relative humidity, it ranged from 14 to 21 days and eggs were deposited at the rate of one every twelve hours until 75 per cent of the total quota was laid, after which they were laid at longer intervals. The number of eggs laid varied from 7 to 44, with an average of 20 during October to January, and 57 during June to August (15.6° to 35° C.). A female living from June 27 to October 27 laid 98 eggs (Rosewall 1930; Finlayson 1932). Candura (1932) reported 50 to 60 eggs in summer and 20 in winter. The postoviposition period was 1 to 24 days, with an average of 9, during October to January. The adults lived from 1 week to 3 months. At 26.7° C. and 65 per cent relative humidity they lived for more than 3 months (Rosewall 1930; Finlayson 1932; Candura 1932).

The eggs are ovoid and translucent with a purplish iridescence. They are usually more or less hidden among or under the food particles (Pearman 1928a; Rosewall 1930).

The incubation period varied from 11 to 27 days, with an average of 21, during October to January, but was 6.9 days during June to August (Rosewall 1930). Candura (1932) gave 4 to 7 days for the

incubation period, depending on the season.

The freshly hatched nymphs are white in color, with the exception of the mouthparts, but become darker after every molt. They underwent three molts in about 30 days (Rosewall 1930; Finlayson 1932).

The life cycle from October to January occupied 93 to 130 days, with an average of 110, while from June to August it took from 24 to 38 days (Rosewall 1930). Candura (1932) reported 21 days in summer and 140 days in winter for the cycle. The insect had six to eight generations per year, and reproduced continuously (Pearman 1928a; Candura 1932).

Kenaga and Fletcher (1942) found that increasing the temperature from a normal of 26.7° to 40.6° C. over a period of 64 hours did not affect any stage of the book louse. The relative humidity, which was 55 per cent, dropped to 40 per cent during this period.

Sheehan (1943) reared it successfully at 27° to 32° C. and 77 per cent relative humidity.

Material and Methods

Book lice were plentiful in the laboratory. They readily collected on Haydak's food mixture, placed in a favorable situation. Covering the food with a crumpled paper towel to decrease light and provide hiding places concentrated them in abundance. The crumpled paper towels were picked up several times a day and shaken over enameled trays 16 inches long, 10 inches wide, and 2½ inches deep, containing similar food and shelter. The outer sides of the walls of the culture trays were smeared lightly with vaseline to keep out mites which were often abundant in the laboratory. These mites fed on eggs but were never seen injuring living adults or nymphs of the book louse. Stock cultures were kept successfully at 32.5° and 30° C. with relative humidity of about 75 per cent. Occasionally high humidity in the chambers resulted in mold growth in the cultures. This did not have any adverse effect on the insect, though its color became deep brown from the ingested mold.

Food Mixture. Haydak's (1936) mixture, with wheat middlings or bran left out, was used as food throughout these experiments. This food was very satisfactory.

Temperature and moisture control. The rearing was done in controlled temperature chambers. Two of the chambers were maintained at 30° and 37° C. with a variation of ± 1°; a third chamber averaged 22° C., but fluctuated from 19° to 22.5°.

Glass-covered pint fruit jars were used for moisture chambers. The required saturation deficiencies were obtained by means of saturated aqueous salt solutions with an excess of salt. Single moisture jars when removed from the temperature chambers were kept covered as much as feasible during examination of the cultures, to avoid extreme changes of the physical environment.

The saturation deficiencies (Buxton 1931) employed, and salts used to obtain them, are given in table I.

Cages. Glass tube cages with round bottoms about ½ inch in diameter and 2½ inches long, having a rim around the upper end, were suspended by a thread in the moisture jars. A rectangular piece of paper towel, slightly smaller than the width of the tube and about half an inch long with adhering food, was placed in the cage. The insects usually remained on the paper, where they fed, molted, and laid eggs. Sufficient food adhered to the

Table I. *Salts employed to obtain the desired saturation deficiencies*

Temperature	Saturation deficiency (mm. of mercury)	Salt (C. P.)
22°C.	3	Potassium chloride
	8	Sodium bromide
	15	Potassium acetate
30°C.	3	Copper chloride
	12	Cobalt chloride
	25	Potassium acetate
37°C.	3	Sodium tartrate
	20	Cobalt chloride
	35	Magnesium chloride

TABLE II. *Measurements of eggs during incubation*

Age of eggs (days)	Number of eggs examined	Length (mm.)			Width (mm.)		
		Average	Extremes		Average	Extremes	
0	25	0.352	0.34	0.38	0.189	0.18	0.20
1	25	0.352	0.34	0.38	0.192	0.18	0.20
2	25	0.352	0.34	0.38	0.189	0.18	0.20
3	25	0.352	0.34	0.38	0.189	0.18	0.20
4	25	0.350	0.34	0.38	0.188	0.18	0.20
5	25	0.353	0.34	0.38	0.189	0.18	0.20
6	4	0.345	0.34	0.36	0.192	0.18	0.20
Average 1–6 days		0.3516	0.34	0.379	0.189	0.18	0.20

paper to last for many days. The paper, however, was renewed at each observation, to provide fresh food and to reduce mold growth. The sides of the tubes were kept clean to check the insects from escaping.

OBSERVATIONS ON THE VARIOUS STAGES

The ovoid eggs are pearly white with purple iridescence when laid, become dull as development proceeds, changing to light yellow before hatching. The chorion is smooth, delicate and membranous, with a bluish pearly lustre. The egg lacks an operculum. At the time of eclosion an irregular longitudinal slit appears at the pointed end which extends to one-third or more of the egg on one side.

At oviposition the eggs are coated with a sticky material with which they adhere to the substratum and to loose extraneous material, depending on availability. It is difficult to remove the egg adhering to a surface without rupturing it.

The eggs are usually laid singly, but as many as six eggs were observed at one spot. The females preferred rough paper for oviposition but will lay eggs in the food material. In general, these observations confirm those of Pearman (1928a),

TABLE III. *Comparative measurements (in millimeters) of different instars*

Instar	Body		Head capsule		Antenna		Tarsal segments
	Length	Width	Length	Width	Length	Segments	
1st	0.421	0.164	0.202	0.164	0.353	9	2
	0.567	0.176	0.214	0.183	0.365	9	2
	0.605	0.164	0.202	0.176	0.365	9	2
Average	0.531	0.168	0.206	0.174	0.361	9	2
2nd	0.769	0.265	0.202	0.189	0.391	15	2
	0.743	0.271	0.214	0.189	0.403	15	2
	0.769	0.277	0.214	0.189	0.416	15	2
Average	0.760	0.271	0.210	0.189	0.403	15	2
3rd	0.970	0.328	0.227	0.227	0.554	15	3
	1.008	0.315	0.239	0.214	0.567	15	3
Average	0.989	0.324	0.233	0.221	0.560	15	3
4th	1.071	0.391	0.252	0.239	0.580	15	3
	1.109	0.391	0.252	0.239	0.592	15	3
Average	1.090	0.391	0.252	0.239	0.586	15	3

TABLE IV. *Measurements of 10 adults (in millimeters)*

		Average	Extremes	
Body	Length	1.193	1.143	1.235
	Width	0.471	0.441	0.504
Head capsule	Length	0.289	0.252	0.302
	Width	0.296	0.281	0.315
Antennal length		0.663	0.630	0.706

Rosewall (1930), and Sheehan (1943). The majority of the eggs are laid on the lower and darker surface of the paper. A piece of paper towel measuring about 1½ inches by 1½ inches was smeared with food and placed in a dish containing adults of the book louse. Eighty-seven per cent of the eggs were deposited on the lower surface, and 13 per cent on the upper surface.

Eggs incubated at 32.5° C. and 85 per cent relative humidity did not change appreciably in size during incubation (table II).

There are typically four molts (Rosewall 1930) but Finlayson (1932) recorded only 3. Freshly hatched nymphs are white, but the color changes progressively from white to light brown with every molt. The body is semitransparent with light brown mouthparts. The early instars may be separated by the number of antennal and tarsal segments and later instars by the body measurements (table III).

The adults are soft-bodied and wingless. They have compound eyes but lack ocelli. The tarsi are 3-, and the antennae 15-segmented. They move in a jerky and halting manner, avoid strong light, preferring dark cracks and crevices. They are usually light brown but sometimes, when feeding on molds, because of their transparent bodies, become brown or red, depending upon the mold color.

Most authors give the length of the adult as about 1 mm. The measurements of ten individuals are given in table IV. All of the adults were more than 1 mm. long. The length of the head capsule was more than the width in all the nymphal instars, whereas the reverse was true with the majority of the adults.

EFFECT OF MOISTURE AND TEMPERATURE UNDER CONTROLLED CONDITIONS

The book louse becomes abundant only under certain environmental conditions. Most workers agree that warm and damp conditions favor its rapid multiplication, and that dry and cold weather checks its abundance. This information is based upon casual observations and little experimental evidence has been available to support these views.

Effect on adults

The adults were kept in cages with pieces of paper towel covered with food,

TABLE V. *Effect of moisture and temperature on pre-oviposition and postoviposition periods*

Temperature	Saturation deficiency (mm.)	Number of females	Pre-oviposition period (days)			Number of females	Postoviposition period (days)		
			Average	Extremes			Average	Extremes	
22°C.	3	35	7.0	4	15	21	55.1	15	280
	8	20	9.4	5	18	12	23.5	14	43
	15	14	x	x	x	14	x	x	x
30°C.	3	22	2.4	1	4	13	13.6	3	48
	12	19	2.6	1	4	17	11.5	2	37
	25	14	x	x	x	14	x	x	x
37°C.	3	21	3.4	1	7	15	41.9	6	82
	20	12	5.7	2	11	11	8.8	3	19
	35	9	x	x	x	9	x	x	x

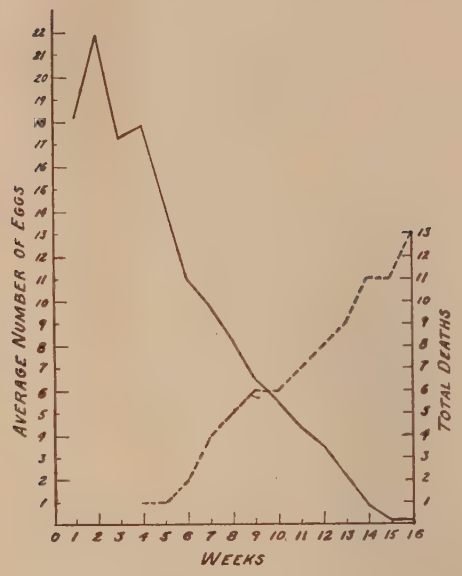

FIG. 1. Average rate of oviposition and number of deaths of 13 females at 30° C. and 3 mm.

at various temperatures and saturation deficiencies.

Pre-oviposition period. The number of days from emergence of adults to first deposition of eggs increased from a low to an intermediate saturation deficiency at all temperatures (table V). The effect of temperature can be better evaluated from the length of the pre-oviposition period at 3 mm. saturation deficiency, which was common to all the temperatures. Theoretically, the difference in the length of the pre-oviposition period at this saturation deficiency should be due to temperature alone (Buxton 1931). The shortest pre-oviposition period occurred at 30° C., suggesting that this temperature was superior for egg development to 22° and 37°.

Rate of oviposition. The average number of eggs laid per female per week by 13 females was determined at 30° and 3 mm. (fig. 1). The weekly average varied from 17.3 to 21.8 in the first four weeks, during which time more than fifty per cent of the eggs had been laid. Oviposition declined rapidly thereafter. The rate of oviposition will, of course, vary under different environmental conditions. There were no deaths during the first three weeks.

Noland (1924) observed only one ripe egg in the ovaries of a female, whereas Finlayson (1932) stated that females oviposited at the average rate of one egg

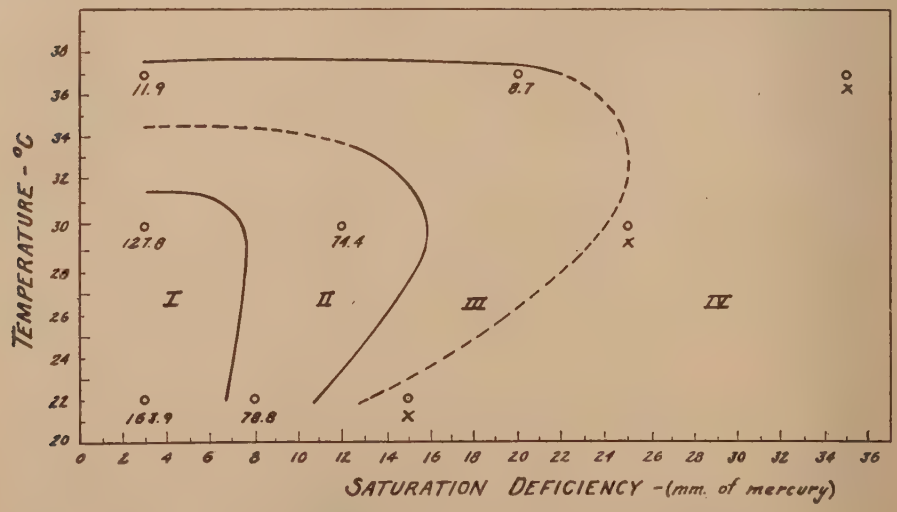

FIG. 2. Average number of eggs laid in controlled environments.

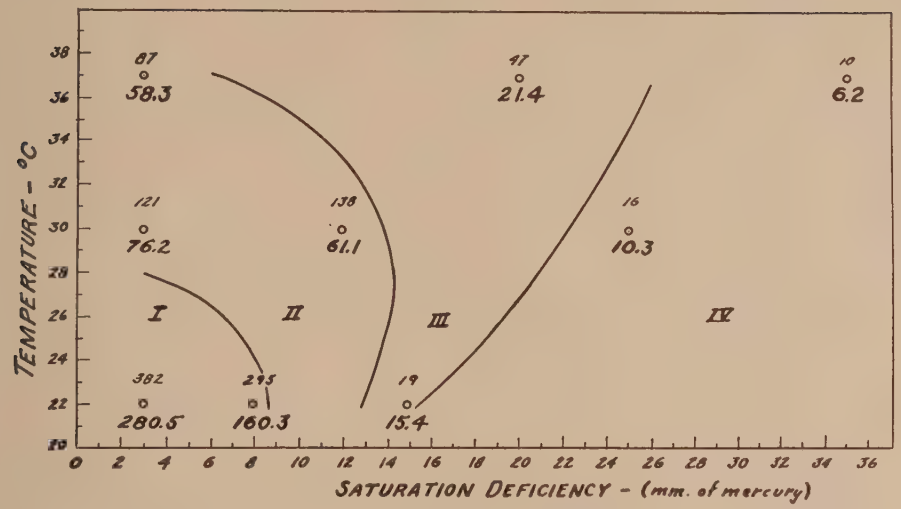

FIG. 3. Longevity of adults in days in controlled environments. Above: maximum longevity; below: average longevity.

in twelve hours at 26.7° and 65 per cent relative humidity.

Oviposition. The average number of eggs deposited per female decreased with a rise in temperature and fall in moisture conditions (fig. 2). Although all the females failed to lay eggs at 15 mm. and 22° yet at 20 mm. and 37° a majority of them (73 per cent) deposited a few eggs. The combined effect of temperature and moisture is shown, although it is evident that moisture was more important at 22°, whereas at 37°, temperature was the major limiting factor. At 3 mm. no female failed to lay eggs at 30°, while 7.4 per cent at 22° and 28.6 per cent at 37° did not lay eggs, showing the unsuitability of 37° (table VI). The greatest number of eggs laid by any female in her lifetime and in 24 hours was 240 and 6, at 30° and 3 mm.

The average number of eggs recorded by Rosewall (1930) and Candura (1932) varied from 20 to 60, depending upon the time of the year, while the maximum number of eggs laid by any female was 98.

The zones of suitability for egg development and oviposition are approximately delimited in figure 2. Zone I represents very favorable combinations of temperature and moisture while zone IV indicates unsuitable conditions.

Postoviposition period. The number of days of survival of females after the last deposition of eggs, unlike the preoviposition period, decreased as the saturation deficiency increased, at all temperatures (table V). Like the preoviposition period, the average postoviposition period at 3 mm. was longest at 22° and 37° and shortest at 30° C.

Longevity of adults. The average

TABLE VI. *Effect of moisture and temperature on oviposition*

Temperature	Saturation deficiency (mm.)	No. of females	Females not laying (per cent)	Greatest number of eggs	
				In lifetime	In 24 hours
22°C.	3	27	7.4	230	2
	8	16	0	231	1
	15	14	100	x	x
30°C.	3	14	0	240	6
	12	20	15.0	127	5
	25	14	100	x	x
37°C.	3	21	28.6	65	4
	20	15	26.7	25	2
	35	9	100	x	x

longevity of adults decreased from a low to a high saturation deficiency, at all temperatures (fig. 3). At saturation deficiencies of 15, 25, and 35 mm. at 22°, 30°, and 37° C., respectively, though the adults lived for a few days they failed to lay any eggs, showing thereby a more detrimental effect of high saturation deficiencies on oviposition than on the length of adult life. The females lived longer at 20 mm. and 37° than at 15 mm. at 22°. This may be due to the difference in the rate of metabolism at these two temperatures. Perhaps at 37°, due to the higher rate, more water of metabolism was being produced which enabled the insect to withstand lower atmospheric moisture at this temperature than at 22°. The longevity of adults also decreased with increase in temperature. The maximum life of any individual was 382 days at 22°.

The zones of suitability for longevity of adults to temperature and moisture are approximately delimited (fig. 3). A comparison of figures 2 and 3 shows a general agreement of temperature and moisture relations for reproduction and longevity. With a change in temperature from 22° to 30° there was a greater reduction in the longevity of adults than in oviposition; while from 30° to 37° oviposition was more reduced than the adult life. This shows that high temperature had more adverse effect on oviposition, as compared to the longevity of adults.

Candura (1932) observed that longevity of adults varied from 1 week to 3 months, while Finlayson (1932) recorded that at 26.7° C. and 65 per cent relative humidity they could live for more than 3 months.

Effect on eggs

The eggs attached to paper were removed from the oviposition cages at intervals of about 12 hours and placed in the desired temperature and moisture environments. They were examined at twenty-four hour intervals to determine the number of nymphs hatching. The nymphs were removed after each examination. Moisture had little effect on the duration of the egg stage (fig. 4). The incubation period, on the other hand, was greatly influenced by temperature, decreasing with an increase in temperature.

The amount of moisture had a very

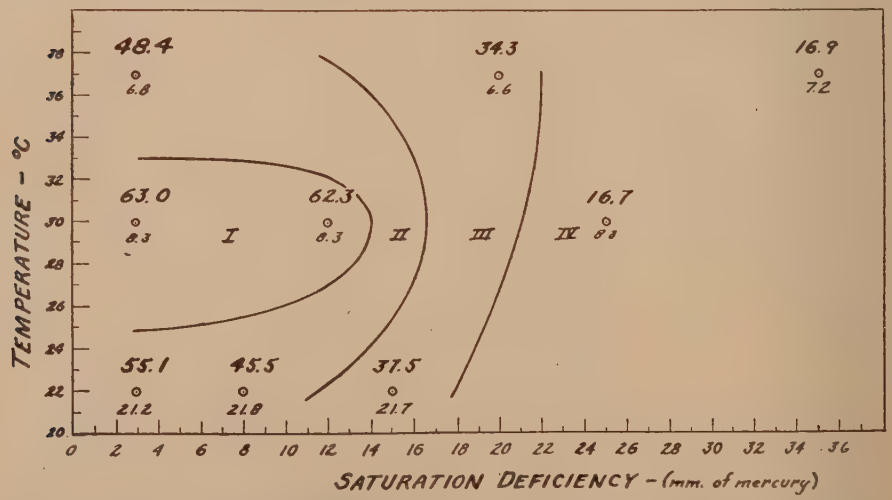

FIG. 4. Average duration of egg stage in days (lower figure) and percentage of viability (upper figure) in controlled environments.

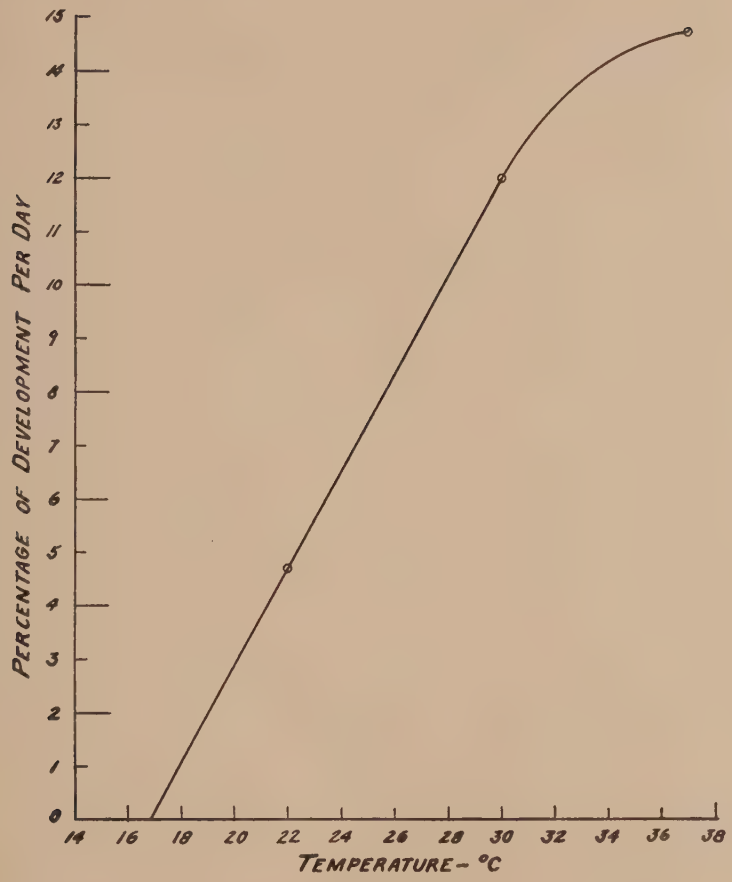

FIG. 5. Velocity-temperature curve of embryonic development.

pronounced effect on the viability of the eggs. At all temperatures the percentage of viability decreased from moist to dry conditions. High saturation deficits of 15 to 35 mm. were unfavorable for incubation and hatching of the eggs. Eggs laid at lower temperatures (30° and 32.5°) and exposed at 37° C. showed a fair percentage of hatch (fig. 4), while those laid at 37° (fig. 2) failed to hatch at all saturation deficiencies. The females were either incapable of laying viable eggs, or the temperature had very adverse effect on the egg in its initial stage of development.

The zones of temperature and moisture conditions suitable for incubation and hatching of the eggs are approximately demarcated in figure 4. However, it must be kept in mind that all eggs developed and deposited at 37° failed to hatch at that temperature regardless of moisture conditions.

The velocity-temperature curve (Sanderson and Peairs 1913) for development of the eggs at 3 mm. is shown in figure 5. The temperature becomes increasingly unfavorable above about 32°. The theoretical threshold of development occurs at about 16.8°.

The values of k at

22° C. = 110.2,
30° C. = 109.6,
37° C. = 137.4.

The values of k for 22° and 30° C. are almost identical, which suggests that the theoretical threshold of development as determined is approximately correct. Normal development would occur from about 18° to 32°.

Effect on nymphs

Freshly hatched nymphs were kept in glass cages with food at the same temperature and saturation deficiency at which they hatched. The nymphs were examined at 24-hour intervals. The duration of the nymphal stage and percentage of nymphs reaching maturity are given in table VII.

The nymphs developed rapidly with a high percentage of survival under moist conditions. While development was much slower at 22° C. than at the higher temperature, the percentage of survival remained as high.

At saturation deficits of 15, 25, and 35 mm. at 22°, 30°, and 37°, respectively, all the nymphs failed to develop into adults. The nymphs died in 7 to 8 days at 22°, 2 to 5 days at 30°, and 1 to 3 days at 37°. During this period there was very little growth in the size of these nymphs. Their abdomens appeared desiccated though head and thoraces seemed to be normal for that size and age. The color was darker as compared to the normal nymphs of the same age. As in the case of oviposition, although 15 mm. at 22° was fatal for the nymphs, the majority of them survived at 20 mm. and 37° due to a combined effect of temperature and moisture. Thus, low moisture had less adverse effect at high than at low temperature, probably because of the higher rate of metabolism at high temperature, as discussed under longevity.

The nymphs hatching from eggs at 22° and 15 mm. were kept at the same temperature and 3 mm., to study the effect of low moisture during incubation on their further development (table VII). This shows that low moisture during the egg stage, and perhaps for a short period during the nymphal stage, appreciably reduced the percentage of survival and increased the duration of the nymphal stage.

It is difficult to demarcate zones of suitability for the development of nymphs, but it is quite obvious from table VII that 3 mm. was favorable at all the temperatures; 8, 12, and 20 mm. less favorable; while 15, 25, and 35 were fatal at 22°, 30°, and 37°, respectively.

The theoretical threshold of development was determined at 3 mm. saturation deficiency as 17.7° C. (fig. 6). That this

TABLE VII. *Effect of moisture and temperature on the duration of nymphal stage and percentage of survival*

Temperature	Saturation deficiency (mm.)	No. of nymphs	Nymphal stage (days)			No. of nymphs	Percentage of survival
			Duration	Extremes			
22 C.	3	26	27.0	24	29	27	96.3
	8	9	29.6	27	31	14	71.4
	15	x	x	x	x	24	0
30°C.	3	26	9.5	9	12	28	92.9
	12	14	10.9	9	14	21	76.2
	25	x	x	x	x	16	0
37°C.	3	24	8.3	6	10	27	88.9
	20	13	12.5	9	18	20	70.0
	35	x	x	x	x	11	0
Nymphs hatching at 22°C. and 15 mm. saturation deficiency							
22°C.	3	8	30.1	27	34	10	80.0

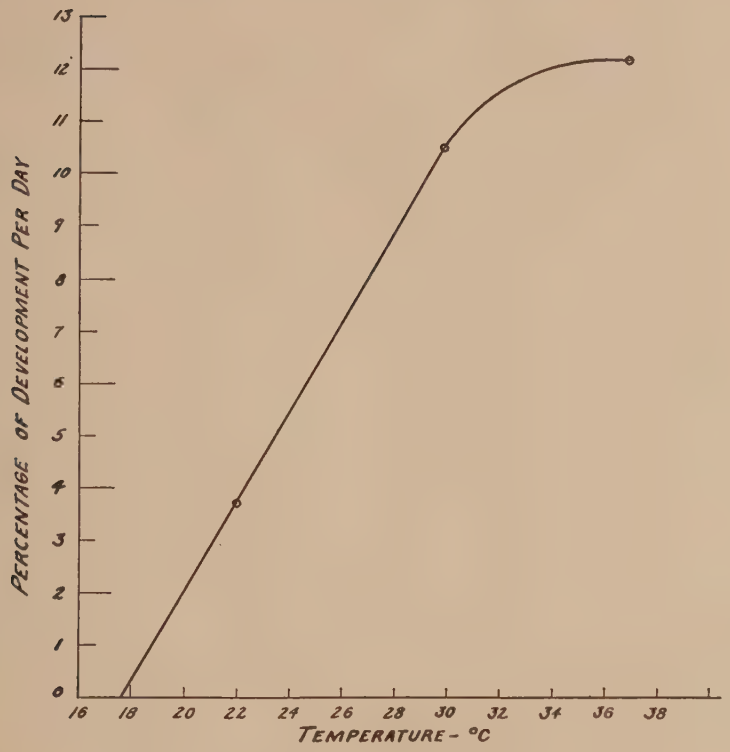

FIG. 6. Velocity-temperature curve of development of nymphs.

point is approximately correct will be seen from the values of k:

22° C. = 116.1,
30° C. = 116.9,
37° C. = 160.9.

The value of k for 37° is widely apart from the other two, as this point was not in the straight line portion of the velocity-temperature curve. Normal development of the nymphs can occur from about 19° to 32° C.

Number and duration of instars

The number and duration of various instars were studied at 30° C. and 3 mm. saturation deficiency (table VIII). It was difficult to find the exuviae of the first two molts, which are very small and white in color. To facilitate their detection, nymphs were liberated in cages on small pieces of paper towels dyed with methylene blue or neutral red and smeared with very finely ground food mixture. The cages were examined every 24 hours for exuviae, which were usually found adhering to the paper.

Among 12 nymphs that completed the nymphal stage successfully nine underwent 4 molts, while three had only 3 molts. In the case of nymphs which molted 4 times, the nymphal period averaged 10.2 days. The nymphs that underwent 3 molts tended to have the instars prolonged, but the nymphal period was 9.9 days, only a little less than those which had 4 instars.

The majority of nymphs (75 per cent) under these conditions underwent 4 molts, which is contrary to the findings of Rosewall (1930) and Finlayson (1932). This might be due to the difference in the environmental conditions under which they carried out their observations, or

TABLE VIII. *Number and duration of nymphal instars at 3 mm. saturation deficiency and 30°C.*

Instars	4 instars				3 instars			
	Number of individuals	Duration (days)			Number of individuals	Duration (days)		
		Average	Extremes			Average	Extremes	
1st	10	3.1	3	4	3	3.3	2	4
2nd	9	2.1	1	3	3	4.3	3	6
3rd	9	2.1	1	3	3	2.3	2	3
4th	9	2.9	2	3	—	—	—	—
Total		10.2				9.9		

they might have missed one molt. As these observations were confined to one set of conditions, the effect of other combinations of temperature and moisture on the number of molts is not known.

SUMMARY AND CONCLUSIONS

The book louse, *Liposcelis divinatorius* (Müller), is a cosmopolitan insect. It is almost omnivorous in habits. It often becomes abundant and causes considerable damage and annoyance.

The ovoid eggs are 0.34 to 0.38 mm. long and 0.18 to 0.20 mm. wide. The freshly laid eggs are smooth and pearly white in color, but change to yellow with age. They do not increase in volume during incubation.

The freshly hatched nymphs are white in color with brownish mouthparts, changing progressively to light brown with every molt. The nymphal instars can be definitely separated. The first instar has 9-segmented antennae and 2-segmented tarsi while the second instar has 15-segmented antennae and 2-segmented tarsi. Both the third and fourth instars have 15-segmented antennae and 3-segmented tarsi. Length and width of the body and head capsule showed a progressive increase from the first to the fourth instar. Typically there were four instars. The average duration of the first, second, third, and fourth instars was 3.1, 2.1, 2.1, and 2.9 days, respectively. The duration of each instar was slightly prolonged, in the few cases where the insect underwent three molts.

The adults are 1.143 to 1.235 mm. long and usually light brown in color. The tarsi are 3- and the antennae 15-segmented. Unlike the nymphs, the width of the head capsule of most of the adults was greater than the length.

Both moisture and temperature affected oviposition. The average rate of oviposition at 30° C. and 3 mm. varied from 17.3 to 21.8 eggs per week during the first four weeks, during which time more than 50 per cent of the eggs had been laid. The heaviest oviposition occurred in zone I, less in zone II, least in zone III, and none in zone IV (fig. 2). Temperature and moisture had a similar effect on the longevity of the adults, though the limits of suitability are somewhat different (fig. 3). The longest life of a female was 382 days at 22° and 3 mm.

The incubation period was little affected by moisture whereas it decreased with an increase in temperature. The percentage of viability decreased with an increase in saturation deficit. The maximum number of eggs hatched at 30° and 3 and 12 mm. The eggs laid and incubated at 37° failed to hatch. A female may lay up to at least 240 eggs. The different zones of suitability for the development of eggs are shown in figure 4. Normal development of eggs can occur from about 18° to 32°.

The duration of the nymphal stage and the percentage of survival decreased with an increase in temperature and saturation deficit. For the development of nymphs saturation deficiencies of 3 mm. were

suitable at all temperatures tested; 8, 12, and 20 mm. less suitable; and 15, 25, and 35 mm. at 22°, 30°, and 37°, respectively, were fatal. A majority of them, however, became adults at 20 mm. and 37° although they failed to do so at 15 mm. and 22°. Normal development of nymphs can occur from about 19° to 32°.

It seems that the capacity of the book louse for reproduction had not been fully realized. Under favorable environmental conditions it can lay a much larger number of eggs and live for a much longer time than hitherto recorded. It can maintain itself in abundance over a wide temperature range. It is more sensitive to moisture than to temperature, and its moisture requirements are not the same at all temperatures, probably due to differences in rates of metabolism. It can endure higher saturation deficits at high than at low temperatures. Its most rapid multiplication will probably occur at about 30° and 3 mm.

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THE COMPOSITION OF THE SUGAR MAPLE–HEMLOCK–YELLOW BIRCH ASSOCIATION IN NORTHERN WISCONSIN

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INTRODUCTION

The mixed hardwood-conifer forest of the northeastern United States and the Lake States in particular has long been the subject of study and conjecture by ecologists and plant geographers. Despite the many papers that have been published few quantitative studies are available describing forest composition of the region in such a way that the findings can be used for comparative purposes. Opportunities for such studies on undisturbed old-growth stands will soon be non-existent in Wisconsin. The field work for the present study was begun in 1941 and completed in 1946. The primary objectives were: first, to record quantitatively the composition of three stands of the relatively undisturbed mature hardwood-conifer forest; and second, to obtain information on the autecology of the climax species. Each of the stands chosen for study are mature communities having representatives of at least four tree species over 150 years of age and each with maximum tree diameters well over 30 inches.

To the writer the expression "community" serves to delimit any particular grouping of plants regardless of successional stage. The term "stand" is used to designate a particular geographic unit of a community or association. The term "association" has in past usage had a tremendous range of meaning varying from a widespread climax type to almost any grouping of plants, large or small, climax or seral in nature. In this paper an association will be considered as a geographically extensive climax community having consistent dominants of the same or closely allied species. It seems reasonable to follow Beard (1944) who defines a climax as ". . . any community which is apparently stable, mature and integrated." A climax community will ordinarily consist of the most mesic species present in the region and those which show the greatest tolerance of shade and of each other. It is not essential for the purposes of this definition that climax species be able to reproduce in their own shade or on the type of litter or soil surface that they produce. Rather they must have the ability to maintain themselves in the mature stand and to bear viable seed successfully. A species will persist in the climax as long as its seed will germinate and its seedlings grow successfully either in the shade of the mature forest or in the constantly occurring natural openings in the forest canopy.

The forest association into which the stands about to be discussed fall is one of several closely related associations [2] which

[1] The writer wishes to express his indebtedness to Dr. J. T. Curtis under whom this study was conducted for his encouragement and stimulating guidance. Sincere appreciation is expressed to those who have assisted the writer in the collection and preparation of this material: Dr. S. A. Wilde for his suggestions and advice on soils matters; Dr. N. C. Fassett under whom this problem was first approached; those members of the U. S. Forest Service who contributed valuable suggestions, notably J. H. Stoeckeler and C. Abrogast of the Lake States Forest Experiment Station and W. W. Intermill, formerly Laona District Ranger; and finally Purdue University for secretarial assistance. Field work on the Tenderfoot Lake stand was greatly aided by the kindness of the late Martin Gillen. Since his death the present owner of this tract, Notre Dame University, has, through Rev. J. J. Reddington, continued to extend the same generous hospitality thus materially expediting this study.

[2] Since this paper was written, McIntosh and Curtis (BULL. ECOLOGICAL SOC. 31: 56. 1950) have proposed the concept of a vegetational continuum for the hardwood stands of southwestern Wisconsin. The continuum concept

FIG. 1. Map of Wisconsin. Crosses show the location of the stands studied: 1—Laona, 2—Tenderfoot Lake, 3—Drummond. The dotted area represents the approximate extent of the sugar maple-hemlock-yellow birch association in Wisconsin.

make up the widespread mixed hardwood-conifer forest. This group of associations seems most accurately and briefly described by the term "northern hardwood forest" (Frothingham 1915b), the boundaries of which are essentially the same as those shown by Nichols (1935) for the eastern hemlock-white pine-northern hardwood region.

The extensive literature on the northern hardwood forest has been reviewed by Nichols (1935) and more recently by Potzger (1946). The careful work of Hough (1936, 1937, 1943), Hough and Forbes (1943), and Morey (1936) in Pennsylvania should be cited. In their consideration of the virgin forest of northwestern Pennsylvania they describe an association very similar to that discussed in this paper. Their conclusions are briefly as follows: "The white pine association is a long-lived subclimax; hemlock-beech is the characteristic climax; beech-maple is a phase of the hemlock-beech climax due to the local absence of hemlock at the present time" and ". . . the absence of hemlock from local areas . . . is explained by evidence of periodicity of hemlock reproduction." Another composition study that should also be mentioned was made by Eggler (1938) on a variant of the northern hardwood forest, the maple-basswood forest type, which is found in Wisconsin and Minnesota along the western edge of the northern hardwood forest.

Location of the Stands

The location of the three stands studied is shown in figure 1. The easternmost area, referred to as the Laona stand, occupies most of Section 18, Township 35 N, Range 14 E, in the southwestern portion of Forest County, Wisconsin. The Laona stand was originally part of a virgin forest of the sugar maple-hemlock-yellow birch association that covered most of Forest County and extended north into Michigan and also east, south and west on the heavy soils of northern Wisconsin. The stand lies 50 or 60 miles west and north of the westernmost extension of beech.

The Tenderfoot Lake stand includes portions of Sections 7 and 9, T. 43 N, R. 8 E located along the northern border of Vilas County, Wisconsin adjoining Michigan. The area consists of two stands of about 25 acres each, two miles apart and separated by Tenderfoot Lake. The data from these two areas have been combined and the areas will be referred to as one unit throughout this paper.

The Drummond area, located in Section 34 of T. 45 N, R. 8 W, consists of

would eliminate the term association at least in its present usage. The writer has grouped the three stands considered here into an association in part to facilitate discussion and comparison. He is, however, in agreement with the principle of the vegetational continuum. There is little doubt that when sufficient stands of the northern hardwoods are examined and analyzed there will be evident a continuous gradation from stands of one "association" to those of any other, depending upon the chance of establishment and the conditions for growth. The three stands described here might well fit into such a continuum series.

a roadside strip several hundred feet wide, bordering state highway 63. This stand in south central Bayfield County, about two and one half miles east of Drummond, is the sole remnant of an extensive forest which originally covered most of the southeastern portion of the county and extended eastward and southward on the heavy soils. Study was confined to the portion of the roadside strip on reasonably well-drained soil. The stand includes a full complement of the species of the sugar maple-hemlock-yellow birch association. It is apparently undisturbed save where a few wind-fallen trees were removed following a severe storm in 1941. Three large pine stumps presumably indicate the entire extent of the lumbering disturbance during the early period of white pine logging. The Drummond area is located very near the western edge of the geographical range of eastern hemlock. Although quantitative material is here presented on only three stands, conclusions are based in part upon experience in a larger number of stands.

Geology, Physiography, and Soils

The underlying bedrock of the region is pre-Cambrian granite, schist or gneiss, highly folded and disturbed but long since reduced to a peneplain with occasional monadonocks. In middle or late Paleozoic time the peneplain was raised until an arch was formed which rises gently from its lowest point in southern Wisconsin to its highest elevation on the Wisconsin-Michigan border.

The visible topography is of glacial origin, and is extremely variable, including morainic hills, drumlins, level and pitted outwash, and recessional and ground moraine. The hardwood stands of northern Wisconsin lie primarily on the morainic formations rather than on the outwash plains.

The Laona stand is on strongly rolling ground moraine, while the Tenderfoot Lake area is on ground moraine associated with the Winegar recessional moraine. The topography is very similar in these areas, consisting of short, choppy hills interspersed with poorly drained valleys. The Drummond area is also situated on ground moraine, not quite so rough, but with the same alternation of level and steeply sloping sites. Approximate elevations above mean sea level calculated from nearby points (Thwaites: *in* Martin 1916) are as follows: Drummond, 1,400 feet; Laona, 1,550–1,650 feet; and Tenderfoot Lake, 1,650–1,750 feet.

Each of the areas is located on podzolic or leached loam soils of the Kennan series (Iron River and Melica series: U. S. D. A.) variants of which cover much of northern Wisconsin (Whitson 1927). Soils of the three areas thus differ only slightly in type from silt loam to fine sandy loam as mapped. Subsurface drainage is largely independent of soil type within a single soil series such as this one.

The various soil types of the Kennan series are each variable in texture due in large measure to the rolling topography. The surface soil may range from coarse gravelly material at the crests of the slopes to a thick layer of fine textured dark colored soil in the valleys. The three areas studied are, in general, well drained but each shows occasional patches of mottled subsoil or boggy places with high water tables. The area of such poorly drained soils is approximately the same in each of the stands, about 15 per cent.

The effects of soil variation within the stands has not been considered since the quadrats were established in a grid arrangement without reference to topography. Sampling of all topographic phases, slope, ridge and valley is necessary to give an accurate picture of the sugar maple-hemlock-yellow birch association. Several workers have stated that minor soil variations do not affect gross species composition within the stand. (Alway and McMiller 1933; Diebold 1935; Hough 1943.) Considerable soil and physiographic variations (areas larger than about one-half acre) especially those concerned with drainage features, do in-

TABLE I. *Summary of climatological data*

	Laona	Tenderfoot Lake	Drummond
Temperature Factors†			
Years of record (to 1940)	12	29	26
January average temp.	14.3°F*	10.7°F	9.3°F
June average temp.	68.6°F*	65.3°F	67.5°F
Last spring frost	May 20	June 3	May 26
First fall frost	Sept. 21	Sept. 10	Sept. 15
Growing season in days	124	104	112
Precipitation Factors			
Average annual precipitation† (inches)	27.99**	30.38	28.85
Total snowfall‡ (inches)	61.1	60.5	77.9***
Total precipitation‡ (inches)	33.85	35.14	34.11

† Data as summarized to 1940 from U. S. D. A. Yearbook 1941, Climate and Man. Weather stations from which records were drawn are as follows: Laona stand from Laona, 8 miles northeast; Tenderfoot Lake stand from Big St. Germain Dam, 20 miles south; Drummond stand from Hayward 30 miles southwest.

‡ Snowfall and total precipitation are given for 1945 only, to indicate conditions that may obtain in a wet year.

* Crandon, twelve miles northwest of the Laona stand, with an 18 year record shows 11.1° F and 66.8° F, respectively.

** Crandon shows 28.96 inches with an 18 year record.

*** P. K. Reservoir, Winter, Wisconsin, 40 miles southeast of the Drummond stand.

fluence composition and these factors have been taken into account so that actual bogs are excluded.

Since, as previously stated, the stands studied have developed on soils quite similar in texture, range of variability, and drainage features, soil differences will not be considered in comparing composition between stands. Intensive soil studies might account for some of the observed differences in stand composition. However, it is very doubtful that the major differences in composition are a result of edaphic factors although the rates of growth may have been influenced.

CLIMATE

The climate of the three areas considered is similar in most respects as might be expected from the relative proximity of the stands. The few differences are readily apparent in table I. Perhaps most important is the shorter and wetter growing season of the Tenderfoot Lake stand in comparison to growing season length and conditions for the Laona and Drummond stands. The Laona and Drummond stands are probably very similar to the stations of reference. The Tenderfoot Lake area is several degrees cooler than the Big St. Germain record indicates.

METHODS

In this study the quadrat method of sampling was used in essentially the same way as in other ecological studies in this region (Daubenmire 1936; Eggler 1938). Square quadrats, 10 meters on each side, were established on a 50 meter grid for the study of arboreal species. All stems over one inch d.b.h. were tabulated. In predetermined corners of each large quadrat two smaller quadrats were laid out, one 2 by 8 meters in size for the study of shrubs and tree reproduction, and the other 1 by 4 meters in size for the study of herbaceous species.

Cores of hemlock, basswood, and white pine were extracted and used to determine age relationships. Unfortunately the majority of trees showed heart rot in varying degrees and in only about 30 cases was it possible to obtain complete cores. Stumps of pine and hemlock, where available in the vicinity, were also counted.

In this study, stand composition is described quantitatively in terms of density, abundance, frequency and dominance as defined below.

Density refers to the number of individuals of a given species present per unit area. The data for tree species is given on a per acre as well as a per quadrat basis to facilitate comparison with other studies. Percentage density figures indicate the relative number of individuals of each species. Calculation simply involves determining what percentage the actual number of trees of a species is of the total number of individuals of all species in the sample.

Frequency is used in the usual sense as the percentage of the total number of quadrats sampled in which the particular species was found.

Abundance figures as used in this paper indicate the average number of individuals of a species per quadrat for the quadrats in which the species occurs. Abundance is calculated by dividing the actual number of trees of a species by the number of quadrats in which the species was found.

The concept of dominance as indicated by basal area designates the important species of the stand from the viewpoint of size. In this paper dominance data are presented as the percentage of the total basal area of the stand. The actual number of square feet occupied by the various species are of interest in that they serve to indicate the bulk of arboreal vegetation actually present. In order to facilitate comparison with other studies the totals are presented in terms of square feet per acre.

The DFD Index (Curtis 1947) is the sum of the percentage density, frequency, and dominance values. By virtue of combining size, relative number and distribution of individuals into one expression the DFD Index becomes an effective method to indicate the relative importance of each species in the stand.

Nomenclature follows that of Gray's Manual (Robinson and Fernald 1908) save where modified by Fassett (1947) or by Tryon *et al.* (1940). Common names are listed with their scientific binomials in a footnote to table III.

The Climax Community

The most important components of any forest community are the members of the arboreal layers. These individuals not only mould their environment, modifying both the edaphic and climatic factors for themselves and their reproduction, but they control almost completely the environment of the lesser plant species. In the discussion to follow, data will be presented to describe the composition of the forest, and to attempt to demonstrate some possibilities concerning the past history of the stands studied. A mental picture should be obtained of the community as a whole before considering the individual species and their relationships.

As one approaches a stand of the sugar maple-hemlock-yellow birch association the first impression is one of a mass of trees within which it is difficult to distinguish any particular individual save perhaps the occasional large hemlock, or more rarely white pine, whose crown stands out over the bulk of the forest. The border of the stand, surrounded by cutover or burned land, is set off by a dense growth of saplings of maple, birch, basswood, aspen, pin cherry and other species which form an almost impenetrable thicket. Over the crowns of these saplings one can discern the large trunks of the mature trees reaching upward into a continuous canopy.

As one enters the forest in the summer the most noticeable change is the tremendous reduction in light intensity, so that, until the eyes become accommodated, the stand seems almost dark. Light seems to filter down from a great height reaching the forest floor in small patches. The stand has a roofed appearance with the main canopy, principally of broad-leafed trees, ranging from the height of 50 or 60 feet upwards to a maximum of 120 feet. The trunks of most trees are straight and

save for hemlock, are clear of branches to the height of 50 feet. Beneath the main canopy there is a second layer which consists of trees (chiefly sugar maple and hemlock) that have been suppressed and whose crowns have not penetrated the upper canopy. Hemlock is relatively inconspicuous during the summer months but displays its presence clearly during the winter.

Below the arboreal layers the stand is quite open save where an occasional large tree has fallen and created a gap in the canopy. In such a spot reproduction of maple and other species forms a conspicuous mass, grading off from the opening in both density and size with the reduction in available light. These thickets form the most obvious part of the shrub layer which otherwise exists merely as scattered stems and low clumps throughout the stand.

The floor of the forest is open and relatively easy to walk through, with both shrub and herbaceous layer generally inconspicuous. Flowering of the herbaceous species is concentrated in a relatively short period during late May and early June, at which time the herbaceous layer attains brief prominence. To one entering the forest from a burned-over area the thick duff layer is impressive. This layer varies from one to three inches in thickness and consists of partially decomposed litter of a friable consistency. Fallen trees varying in size from small saplings to logs well over 30 inches in diameter are found in all stages of decay, while an occasional stub or broken trunk stands upright, riddled with woodpecker holes and generally bearing several large polypores. Fungi are abundant on the ground also. There is relatively little air movement in the forest, resulting in an atmosphere of remarkable quiet and heightened humidity.

As one becomes accustomed to the reduced light in the stand, the component species attract attention. Sugar maple is most evident both in number of stems and regularity of distribution throughout all size classes. Hemlock occurs in small groups, often forming an extremely dense canopy under which there is a thick mat of needles with but little vegetation of any kind. Sometimes the hemlock clan is so dense that other species are completely excluded and large enough so that neighboring hardwoods cannot form an overlapping canopy. In such a case the hemlocks form a very conspicuous island-like grouping. Large hemlocks 30 to 36 inches d.b.h. are occasionally present as dominant trees, but more often hemlock is a part of the second arboreal layer.

Yellow birch, which occurs as single individuals through the stand, is remarkable in its consistently large size as well as in its even distribution. Basswood is less frequently observed, often growing in clumps of several stems formed as stump sprouts. There are a few single trees of large size; pole size trees are present, as are saplings, in small numbers. Other less abundant tree species include elm, ash, and white pine.

TABLE II. *Summary of data on tree species of the sugar maple-hemlock-yellow birch association based on the combined data of the Laona, Tenderfoot Lake, and Drummond stands*

Species	Per cent frequency	Per cent density	Per cent dominance	D.F.D. index†
Sugar maple	89	41.8	28	158.8
Hemlock	67.6	22.3	23.8	113.7
Yellow birch	58.6	8.7	24.9	92.2
Basswood	51.3	8.9	13.9	74.1
Ironwood	34.6	7.4	0.7	42.7
Balsam fir	31.4	5.8	0.6	37.8
American elm	10.6	1.9	2.0	14.5
White pine	5.4	0.6	4.8	10.8

† D.F.D. Index is the sum of the per cent density, frequency, and dominance for each species.

The Tree Layer

The general composition of the arboreal layers of the sugar maple-hemlock-yellow birch association is shown in table II. Examination of the following tables (tables III, IV, V and VI) reveals that although the three stands examined differ somewhat they are sufficiently similar to justify grouping them into a single association.

The tremendous numbers of young sugar maples and the apparent lack of hemlock and yellow birch seedlings on the forest floor might lead one to believe that sugar maple will soon form pure stands throughout the extent of the present sugar maple-hemlock-yellow birch association. Table VI indicates that sugar maple seedlings are about 100 times as abundant as those of hemlock or basswood and more than 30 times as abundant as yellow birch seedlings. It is apparent that there must be tremendous mortality in the maple, which would necessarily be the case even if it were the only species present.

Only occasionally does a maple seedling survive to sapling size under the closed canopy so that when an opening does occur in the canopy the seedling is in a position to take advantage of the increased light. In many cases the opening produced is quite large, such as might be formed by the death of a large tree which on falling carried with it several of its smaller neighbors, and the seedlings or saplings already present are not abundant enough or vigorous enough to occupy the opening completely. In these cases the seedlings for several years following, both

Table III. *Dominance of tree species*†

Species‡	Stand			
	Laona	Tenderfoot Lake	Drummond	Average
Sugar maple	36.7	22.3	25.2	28.0
Hemlock	22.7	18.3	30.4	23.8
Yellow birch	19.2	34.2	21.2	24.9
Basswood	11.6	15.4	14.4	13.8
White pine	5.0	5.8	2.8	4.8
American elm	4.2	0.79	0.87	2.0
Ironwood	0.29	0.28	1.6	0.7
Balsam fir	0.29	0.75	0.68	0.6
Paper birch	—	—	1.9	0.6
Mountain maple	—	—	0.01	—
Blue beech	—	—	0.04	0.01
Red pine	—	—	0.65	0.22
White ash	—	1.3	0.18	0.5
White cedar	—	0.97	—	0.3
Red maple	—	—	0.06	0.02
	100%	100%	100%	100%
Total basal area (square feet per acre)	246.8	269.2	283.2	266.4
Quadrats used as basis	35	30	27	
Total acreage of quadrats	0.86	0.74	0.67	

† Percentage of total basal area including all trees over 1 inch d.b.h.

‡ Common names and binomials of arboreal species are as follows: (Northern) White pine—*Pinus strobus* L.; Red (Norway) pine—*Pinus resinosa* Ait.; White spruce—*Picea canadensis* (Mill) BSP.; Balsam fir—*Abies balsamea* (L.) Mill.; (Eastern) Hemlock—*Tsuga canadensis* (L.) Carr.; (Northern) White cedar—*Thuja occidentalis* L.; Aspen—*Populus tremuloides* Michx.; Ironwood (Hophornbeam)—*Ostrya virginiana* (Mill.) K. Koch.; Blue beech—*Carpinus caroliniana* Walt.; Yellow birch—*Betula lutea* Mich. f.; Paper (White) birch—*Betula papyrifera* Marsh; American elm—*Ulmus americana* L.; Choke cherry—*Prunus virginiana* L.; Pin cherry—*Prunus pennsylvanica* L. f.; Mountain maple—*Acer spicatum* Lam.; Sugar maple—*Acer saccharum* Marsh.; Red maple—*Acer rubrum* L.; Basswood—*Tilia americana* L.; White Ash—*Fraxinus americana* L.

TABLE IV. *Per cent densities of tree species*

Species	Trees over 10 inches d.b.h. only			All trees over 1 inch d.b.h.		
	Laona	Tenderfoot Lake	Drummond	Laona	Tenderfoot Lake	Drummond
Sugar maple	43.6	24	22	45.3	42	38.1
Hemlock	27.7	18.8	33.9	21.4	26.5	18.7
Yellow birch	15.9	28.1	22.9	6.1	10.7	9.5
Basswood	7.5	21.9	13.7	8.6	8.8	9.2
Balsam fir	—	—	0.9	8.9	5.0	2.9
Ironwood	—	—	—	3.7	3.2	15.2
White pine	2.1	2.1	1.8	0.61	0.63	0.63
American elm	3.2	0.3	1.8	4.9	0.3	0.63
Mountain maple	—	—	—	0.61	0.63	0.95
White ash	—	1.0	—	—	0.31	0.32
Blue beech	—	—	—	—	—	1.9
White cedar	—	3.1	—	—	1.9	—
Red pine	—	—	0.9	—	—	0.3
Red maple	—	—	—	—	—	0.3
Paper birch	—	—	1.8	—	—	0.63

of maple and other species, have a far better chance for survival. This condition results in dense thickets of saplings, all growing rapidly and competing vigorously for space in which to enlarge their crowns and root systems. If the opening formed is small, one or several of the large trees may soon spread into the space closing the crown and most of the saplings then succumb.

Hemlock cores examined indicate that some trees started slowly under dense shade; others started in the open as evidenced by their rapid growth at the start slowing later as a result of suppression by faster growing hardwoods. The presence of a number of large dead hemlocks could be taken to indicate that hemlock is passing from the stand. However, the prime effect is a drop in basal area and not in density since the number of large trees is small. Lutz (1930b) has pointed out that a young stand of hemlock will exclude seedling reproduction, both of hemlock and other species, for a long period due to its great density. This can be observed in a number of quadrats in each stand but is especially evident at Drummond. There in several cases there were six trees or more over eight inches d.b.h. in a quadrat, and in each instance the ground flora was sparse and reproduction absent. In extreme cases, with over 10 hemlocks per quadrat, vegetation was completely absent from the forest floor.

The relative absence of hemlock in the seedling stage and the small number of trees in the 1 and 2 inch classes is evident in each stand. Other investigators have noted the same situation. Gleason (1924) states: "Records . . . extending over a period of 13 years . . . indicate that reproduction of hemlock is very rare, and the general deficiency of hemlock saplings show that this condition has prevailed for years." Deficiency of hemlock seedlings in recent years can be attributed in part to heavy browsing pressure by deer (Swift 1948).

Although infrequent, there is some reproduction present; in the stands examined approximately 1 quadrat in 10 contained hemlock seedlings. However, reproduction is not visible in the amount suggested by Nichols (1918) in New England where he speaks of hemlock and maple seedlings together carpeting the ground. In most instances in this study the young seedlings were observed growing upon rotting logs or stumps (apparently the favorite site for both hemlock and yellow birch seedlings). This has been observed by several workers including, Harlow (1900), Lutz (1930a),

Hough (1943), and Potzger (1946). The seedling growing on an old log sends out an extensive root system. In the case of hemlock, these roots, instead of passing into the adjoining soil or leaf mould, restrict themselves almost entirely to the rotten wood and may extend several feet in each direction within its limits. The main roots are extensively branched with numerous mycorrhizae and are frequently covered with a yellowish mycelium. The limitation in root habitat seems to persist at least until the seedling has developed into a sapling several feet in height. Mature trees of both hemlock and yellow birch are often found with the recognizable, although highly decayed, remains of the log, upon which they began their existence, still present within the confines of their roots. Some authors attribute the ecesis of yellow birch and hemlock on old logs to a greater availability of moisture, sustained throughout the growing season by the organic nature of the substrate and the abundant moss covering. The moss covering is, in itself, an indication of favorable moisture conditions. This may be the answer although there is also the possibility that the organic substrate is more favorable for the mycorrhizal associates of the species. Surely a basic difference must exist between the seedling requirements of sugar maple on the one hand and hemlock and yellow birch on the other, for the maple reproduction covers the ground between logs, whereas hemlock and yellow birch seedlings are restricted to the old logs themselves. This condition can be observed in any of these stands and deserves further investigation.

Determination of age in hemlock proved to be quite difficult and the use of increment cores was found unsatisfactory. In 60 to 70 per cent of the trees bored it proved impossible to get a sound core due to the presence of an unidentified wet rot or of a completely hollow center. Ages determined from cores, and stump counts (a more satisfactory source), varied from 53 years for a tree 1½ inches d.b.h. to 370 years for a tree of 27 inches d.b.h. Work with these cores and stump counts and with age-diameter data from other sources indicated that the correlation of age with diameter is unreliable, particularly for use in interpreting relative ages of individuals and groups. Marshall (1927) in Massachusetts and Morey (1936) in Pennsylvania both indicate that the dispersion of age-diameter data is so great that accurate estimation of age based on d.b.h. is not feasible.

The distribution of hemlock diameters for trees in these stands shows a peak in density at approximately four inches d.b.h. (Stearns 1947). The cause for this peak cannot be demonstrated here although it is possible that it indicated a period during which hemlock reproduction was considerably more abundant than it has been for some years since. A detailed study of age distribution by Hough (1943) showed conclusively that time of hemlock seedling establishment in Pennsylvania at least, was periodic. This seems to be the case in Wisconsin also.

Climatic shifts and natural catastrophe are held largely responsible for the periodicity in hemlock (Hough 1936, 1943) although factors of site and age undoubtedly influence seed production and seedling establishment. Where hemlock exists in clans or dense groups, it is probably a result of mass establishment following some occurrence which not only opened up the forest canopy but which also coincided with favorable seed years and favorable climatic conditions. The preference of hemlock for very moist situations, stated by Westveld (1933), does not apply to the climax type but rather to the occurrence of the species in pure stands. This may be related to the increased frequency of heavy windfall in shallow rooted trees as well as with the moisture requirements for seed germination. The occurrence of hemlock in the stands studied was analyzed statistically and showed no relationship to the amount of slope.

Periodicity in other species is also sus-

TABLE V. *Density‡, frequency, and abundance data† for tree species*

	Sugar maple	Hemlock	Yellow birch	Basswood	American elm	Ironwood	Balsam fir	White pine	Other tree species*	Total all species
Laona										
Density	4.23	2.0	0.57	0.8	0.46	0.34	0.83	0.06	0.06	9.35
Frenquency %	91.4	62.9	42.9	48.6	20	17.1	45.7	5.7	—	—
Abundance	6.2	3.2	1.3	1.65	2.3	2	1.8	1	—	—
Density/Acre	172	81.4	23.2	32.6	18.6	14.0	33.7	2.3	2.3	380.1
Tenderfoot Lake										
Density	4.43	2.8	1.13	0.93	0.03	0.33	0.53	0.07	0.3	10.55
Frequency %	83.3	73.3	70	46.7	3.3	20	30	6.7	—	—
Abundance	5.3	3.8	1.6	2	1	1.6	1.8	1	—	—
Density/Acre	179.7	113.5	45.9	37.8	1.3	13.5	21.6	2.7	12.2	428.2
Drummond										
Density	4.44	2.19	1.11	1.15	0.07	1.78	0.33	0.07	0.52	11.66
Frequency %	92.5	66.7	6.3	59.2	8.4	66.7	18.5	3.7	—	—
Abundance	7.5	3.3	1.75	1.8	1	2.7	1.8	2	—	—
Density/Acre	179.1	88.1	44.8	46.3	3.0	71.6	13.4	3.0	20.9	470.2
Average for three stands										
Density	4.36	2.32	0.93	0.95	0.21	0.76	0.59	0.06	0.27	10.45
Frequency %	89	67.6	58.6	51.3	10.6	34.6	31.4	5.4	—	—
Abundance	4.95	3.4	1.6	1.8	1.9	2.1	1.8	1.2	—	—
Density/Acre	176.6	93.8	37.0	38.3	8.3	30.8	23.8	2.6	11.0	422.2

† Density data are presented here as trees per quadrat.
‡ These data include all individuals over one (1) inch d.b.h. Sample size is as indicated in table III and text.
* Species included in this category are listed in table IV.

pected although little evidence is available. A low point which occurs at about 6 inches d.b.h. in maple diameter distribution may be evidence of a period unfavorable for maple reproduction, or a period during which all maple reproduction for some years previous was killed. The fact that this low point occurs in more than one or two stands indicates that it is not a purely local phenomenon but is more likely the result of some widespread climatic occurrence.

Yellow birch is quite irregular in the establishment of its reproduction. Local situations such as heavy windfall or partial cutting result in greatly increased reproduction. Some seed is produced almost every year, but in occasional years tremendous quantities are shed. This habit of irregular seed production is shared by the other species of this association.

The presence of an occasional large yellow birch, the relatively high basal area of the species, and the small number of stems present (tables III, IV, and V) all reinforce the description of the species as one which usually occurs in this type of stand almost entirely as mature individuals with few if any pole size trees or saplings. The reasons for this are not well understood. Graham (1941) states that yellow birch is apparently unable to establish itself as satisfactorily in the thick leaf mould and deep shade of the forest as it does on exposed soil or recent burns. He suggests that the present old yellow birches are relics of a widespread successional change following severe drought and fires occurring about 1550. The work of Zillgitt and Erye (1945) substantiates the requirements for yellow birch reproduction suggested by Graham. They state that yellow birch is a good seeder but develops best where the humus is scarified or disturbed and further that reproduction is most successful when the openings made in the stand are

about 1/10 acre in size. Westveld (1933) states that "The large proportion of yellow birch in the dominant stand probably is due in part to its fairly rapid growth which gives it an advantage in getting into the upper canopy. Furthermore, when it is forced into the intermediate layer, its intolerance prevents its survival." Reproduction of yellow birch, although with a density per acre greater than any other species save sugar maple, is still not common and much of it is of very small size (table VI). Reference to field notes indicates that over 40 per cent

TABLE VI. *Reproduction of tree species*

Species	Height classes								All sizes	
	0–12″		13–36″		37–72″		Over 72″ and under 1″ d.b.h.		Density	Density/ acre
	Density†	Freq. %	Density	Freq. %	Density	Freq. %	Density	Freq. %		
Sugar maple										
Laona	6,842	91.4	897	80	268	34.3	37	17.1	8,044	20,362
T. Lake	11,956	100	3,533	96.7	173	33.3	50	6.7	15,712	39,780
Drum'd	7,981	100	2,181	92.6	315	55.6	122	37	10,599	26,823
Hemlock										
Laona	126	11.4	6	2.9	3	2.9	—	—	135	340
T. Lake	13	6.6	—	—	—	—	—	—	13	34
Drum'd	96	3.7	11	3.7	—	—	—	—	107	272
Yellow birch										
Laona	231	31.4	169	25.7	23	14.3	—	—	423	1,070
T. Lake	463	13.3	3	3.3	—	—	—	—	466	1,181
Drum'd	4	3.7	7	3.7	—	—	—	—	11	28
Basswood										
Laona	23	14.3	29	22.9	14	8.6	—	—	66	166
T. Lake	90	13.3	33	20	—	—	—	—	123	312
Drum'd	156	37	111	33.3	11	11.1	—	—	278	712
Elm										
Laona	29	14.3	26	14.3	17	5.7	6	8.6	78	195
T. Lake	7	3.3	—	—	—	—	—	—	7	17
Drum'd	—	—	4	3.7	—	—	—	—	4	9
Ironwood										
Laona	11	5.7	11	8.6	6	2.9	—	—	28	72
T. Lake	10	6.6	3	3.3	—	—	—	—	13	34
Drum'd	44	25.9	41	22.2	11	11.1	—	—	96	244
Balsam fir										
Laona	9	8.6	—	—	—	—	—	—	9	22
Drum'd	22	11.1	7	7.4	4	3.7	—	—	33	84
Other species‡										
Laona	211	—	177	—	51	—	—	—	439	1,113
T. Lake	237	—	70	—	7	—	—	—	314	792
Drum'd	211	—	159	—	22	—	4	—	396	1,004

Total density per acre: Laona, 23,340; Tenderfoot Lake, 42,150; Drummond, 29,176.

† Density figures represent the number of individuals per 100 quadrats 2 × 8 meters in size (*i.e.*, 1,600 square meters). The actual size of the sample is as follows: Laona, 35 quadrats, 0.138 acre; Tenderfoot Lake, 30 quadrats, 0.118 acre; and Drummond, 27 quadrats, 0.107 acre.

‡ Other species include mountain maple abundant in all three stands, blue beech and red maple prominent in the Drummond stand, and white ash in greatest numbers in the Tenderfoot Lake stand but also present in the Drummond stand. Choke cherry, the other species included, was found in considerable amounts in several openings in the Laona stand. No paper birch, red pine, or white cedar reproduction was noted in these stands. Only one white pine seedling was observed, that in the Drummond stand.

of the yellow birch reproduction in the 0 to 12 inch class consisted of seedlings under 2 inches tall.

Yellow birch is found in small numbers in almost all variations of the northern hardwood forest. The ability of the species to germinate and grow successfully in exposed situations accounts for the fact that occasionally a much higher percentage of yellow birch is observed than might ordinarily be expected. This may be attributed to widespread windfall, fire or perhaps both.

The large size of most of the basswood in the stand has been noted. Data presented by Frothingham (1915a) and by Zon and Scholz (1929) indicate that basswood is the fastest growing species of the climax. Basswood reproduces itself in the climax stand largely by means of stump sprouts. These sprout trees however have a limited life span as a result of heart rot (Hepting and Hedgcock 1937). In many instances large trees as big as 20 inches d.b.h. which are obviously sprouts were seen growing in clumps of two to five. A sprout of 6 to 8 inches will occasionally be found growing on a tree as large as 30 inches d.b.h. Basswood seedling reproduction is apparently not common. The seedlings require more light than is usually available. The largest, healthiest trees seem in most cases to be of seedling origin, resulting from the coincidence of the formation of large openings in the canopy with or shortly following a year in which a large basswood seed crop was produced.

Even-aged establishment of basswood was observed in the Springstead Lake stand in southern Iron County. Here a recent logging operation removed about 60 per cent of the merchantable volume of the stand and disturbed the humus layer considerably. In the summer of 1946 this stand averaged about 150 basswood seedlings per 100 square meter or about 36,000 seedlings per acre, all within a range of one to three years of age. These seedlings originated from seeds already present in the duff at the time of cutting.

Before definite periodicity of any species can be demonstrated in northern Wisconsin extremely detailed age studies will be necessary. Such a study should be made, in the near future, on the logging operations now in progress or just completed in old-growth stands. Much more careful work is necessary on the autecological relationships of all the tree species.

White pine as an indicator of stand history

The history of these stands is necessarily largely a matter of conjecture. There is no written record of sufficient antiquity and far too little information on the relative ages of the component individuals of the stands to support a detailed history. A sound white pine in a stand is one of the best sources of information available. At first glance it would seem that such ocasional individuals are relics of some widespread earlier stage in the succession. These earlier successional stages are commonly seen today as pure stands of white pine which became established after cutting and fire on sandy or loamy soils. This relict concept is not new; Whitford (1901) expressed it clearly and most workers since have agreed with his interpretation. Hough (1943) holds the same view, with some modification. He states, "Intensive analysis of age distributions in East Tionesta, Heart's Content, Cooke Forest, and many second growth stands, reveals white pine to have originated as even-aged stands or in a few cases as successive even-aged groups—as a result of catastrophes which practically wiped out, or opened up the preceding stands. Droughts followed by forest fires are known to have been the catastrophic agents in some cases, windthrow in others." Nichols (1935) on the other hand suggested that white pine occurred as scattered individuals of uneven age in mixtures with the hemlock and climax hardwoods originating there

". . . in relatively small forest openings brought about by windfall or some other purely local influence." If in even-aged groups or in quantity, Nichols agrees that white pine is a result of a major catastrophe.

Observations by the writer in northern Wisconsin indicate that white pine is generally present in the climax in small numbers. In the Tenderfoot Lake stand, two pines were recorded in nearby quadrats about 200 feet apart and cores showed them to be approximately the same age, about 180 years. These trees were probably remnants of a group that had seeded into a spot burn of a windthrown area an acre or two in size. Most of the hardwood trees present in the vicinity are about the same age as the pines and it is doubtful that any in the immediate vicinity are older. Lightning fires are known to be responsible for small even-aged patches of pine in the west and it is entirely possible that the same applies here. The seed source for these two trees may have been any one of several different groups of older pines present within a half mile radius. A section from one of these older pines was examined and found to be aproximately 400 years old (Stearns 1950).

The fact that both near the Laona stand and the Tenderfoot Lake stand veteran white pines have been present for 400 years with little reproduction save on swamp edges and ridge tops indicates that more than incidental windfall openings are necessary to permit pine to come into the closed stand. When pine does get the requisite opportunity a group of trees probably becomes established although most of them are shaded out at a very early age by more rapidly growing hardwoods which enter the opening at the same time. These hardwoods may include aspen, paper birch and pin cherry as well as climax species, those present depending upon weather conditions and seed available at the time. The rapid growth rate of the pine will keep its crown in the upper arboreal layer provided that it is not suppressed by the hardwood species during the first few years.

This spot establishment of pine is of rare occurrence but, since pine is extremely long-lived, chances for conditions necessary for spot establishment within an area at least once during every 200 or 300 year period are fairly good. The places where pine is most commonly found in the climax community, such as steep slopes and ridge tops, swamp edges and lake shores, are those where suitable conditions such as extensive windfall and disturbance or removal of the duff layer are most likely to occur. In such locations more light is provided on the forest floor as a result of small windfalls than is the case on more level topography.

Comparison of stand history

It is probable that differences in history of the three stands examined account in large measure for the variations in species composition. The Laona stand is the oldest of the three from the point of view of undisturbed development. It lacks the various subclimax species, paper birch, red maple, and red pine, that are present in the Drummond stand and the Tenderfoot Lake stand. The largest individuals of four of the most important trees species, are found in the Laona stand (table VII). There are 44 stems

TABLE VII. *Maximum d.b.h. (inches) of tree species*†

Species	Laona	Tender-foot Lake	Drummond	Maximum for species
Sugar maple	29	31	24	31
Hemlock	33.5	29	31.5	33.5
Yellow birch	28	36.5	28	36.5
Basswood	38	21.5	26	38
American elm	29	17	13	29
Ironwood	6	5	7.5	7.5
Balsam fir	4.5	9	12	12
White pine	36	33.5	28	36
White ash	—	21.5	8	21.5
White cedar	—	10.5	—	10.5
Red pine	—	—	15	15
Paper birch	—	19	—	19
Maximum diameter for stand	38	36.5	31.5	38

† Maximum diameters listed are only for trees present in quadrats.

per acre over 20 inches d.b.h. in the Laona stand, compared to 28.3 and 37.6 at Tenderfoot Lake and Drummond, respectively (table VIII). In addition to the large trees recorded there appear to be many more large windfalls on the forest floor at Laona than in the other two stands, a further indication that the Laona stand reached a stable condition at an earlier date.

The study of the surveyor's field notes substantiates this description of the Laona stand. Composition shown in 1857 differs from that today only in a slight reduction in the amount of hemlock and a slight increase in the amount of maple and basswood over the 90 year period (Stearns 1949). No evidence of fire was seen in the stand save for a possible fire scar at the base of a large white pine. This scar may be the result of a small lightning fire since the tree carries a healed scar 50 feet long on the lower trunk.

The even gradient in numbers of trees in the various size classes (table VIII) is also indicative of a stabilized stand. The Laona stand has probably suffered no serious disturbance, within the confines of the area studied, for at least 250 years and possibly somewhat longer. Here, as well as in the Tenderfoot Lake area and many other places in northern Wisconsin and Michigan, occasional living white pines and hemlocks are found approximately 400 years in age. It has been suggested by Graham (1941) that these trees may well be relics of stands whose origin dates to a tremendous series of fires during the 1500's.

The Tenderfoot Lake stand is probably also an old stand. However, there is a large proportion of yellow birch and basswood, shown both in the dominance and in the percentage of total density of these species in the larger size classes (tables III and IV). This is an indication that this stand has suffered some considerable disturbance at a period more recent than the one dated by the 400 year old trees. The presence of a few large white spruce and some white cedar is further indication of disturbance. It may be that following the extensive fires of the 1500's the area was taken over by spruce [3] and cedar invading from the swamp margins with pine present in an occasional even-aged patch while the hardwood species reforested the area more slowly from small scattered remnants. Heavy windfall of spruce and cedar probably aided the establishment of yellow birch and basswood. It should be noted that white spruce is now pioneering on cut-over lands in the vicinity of Tenderfoot Lake. Hardwood superiority was regained sev-

TABLE VIII. *Density per acre by diameter classes for all trees of all species over one inch d.b.h.*

Diameter class	Laona	Tenderfoot Lake	Drummond	Average density
1–3.9 in.	186.3	152.5	226.4	188.4
4–9.9 in.	83.3	145.7	82.5†	103.8
10–23.9 in.	86.8	109.3	146.9	114.3
Over 24 in.	22.0	20.2	16.5	19.6
Density over 1 inch d.b.h.	378.5	427.8	472.3	426.2
Density over 10 inches d.b.h.	108.8	129.5	163.4	133.9
Density over 20 inches d.b.h.	44.0	28.3	37.6	37.0

† Low figure is a result of either hemlock establishment and no reproduction or of relative drought for a long period.

[3] White spruce in Wisconsin is not truly a bog tree. It grows on poorly drained upland soils from northern Vilas county northward and has been fairly satisfactory for replanting purposes on some of the popple areas in Forest county, on heavy soil. Jackson (1914) reported it in mixture with Cedar-hemlock-balsam fir on wet sites high in organic matter. It probably survived fire on these marginal sites, some of which are surrounded by bog, in the Tenderfoot Lake region.

eral hundred years ago since much of the large basswood now present is of sprout origin. The 180 year old pines and associated hardwoods previously mentioned represent at least a minor disturbance. There may have been some disturbance of this stand during the white pine logging period in the 1890's but, if so, it was slight and is no longer evident. Recent small changes from normal "virgin" condition have occurred largely as a result of increased windfall due to the opening up of the edge of the stand by roads and fire lanes.

The Drummond stand is similar to the Tenderfoot Lake stand in appearing to have suffered some sort of major disturbance within the past several hundred years. The evidence rests in part upon the number of non-climax species present, including red pine and paper birch, and on the peculiar distribution of densities in respect to diameter classes (table VIII). Instead of a more or less regular reduction in density progressing from a smaller to a larger size class, we find a pronounced increase in density in the 10 to 20 inch class over the density in the 4 to 10 inch group. The high percentage of hemlock is difficult to explain and is probably largely a matter of some particular chance of stand origin. Two white pines in the area give a probable clue to the date of the disturbance since both are about 200 years old. The hemlock at Drummond shows a greater tendency to form clumps than in the other stands. Whitford (1949) has suggested that the ratio of abundance to frequency, A/F ratio, may serve as a relative measure of contagiousness. A high ratio indicates that the species has a tendency to be grouped and thus show a non-random distribution. Examination of the A/F ratios in the three stands indicates that hemlock is most evenly distributed in the Laona stand, shows the greatest aggregation for trees of all diameters in the Drummond stand, and in the Tenderfoot Lake stand also shows strong non-random distribution, especially in trees over 10 inches d.b.h. The differences in evenness of distribution were observable in the field. Where hemlock occurs in groups it presumably became established on exposed mineral soil [4] with an abundance of light rather than on logs in the shade of a climax stand. These pure clumps of hemlock at Drummond are still very dense and a study of cores show them to be relatively young (*i.e.,* 180–200 years).

It is possible that the bulk of the Drummond stand dates back to a fire, tornado or similar catastrophe about 200 years ago. The small number of old pines, whose presence is not indicated by weathered stumps, were probably veterans whose establishment dated back to the disasters of the 1500's. The proximity of this stand to the sandy areas of Bayfield County might account for more fires since the pineries are known to have burned occasionally. Light fire following a heavy windstorm in the period 1740–1770 could best explain this mixture of younger pine, hemlock, and hardwoods of approximately the same age.

The Shrub Layer

Consideration of the shrub layer can be brief; since sugar maple, the most common species found as a transgressive in this layer (table IX), has already been discussed. Other tree reproduction enters into the composition of this layer with ironwood and yellow birch as the principal species. Mountain maple and blue beech, listed previously as small trees, are often classed as members of the shrub layer.

Only a few species of shrubs are present in this association. Of these, *Dirca palustris,* leatherwood, is the most characteristic shrub of the sugar maple-hemlock-yellow birch association in the Lake

[4] The most successful hemlock reproduction—*i.e.,* abundance and vigor, has been on mineral soils, road cuts, swamp edges, etc. The density of the hemlock at Drummond, the lack of old logs and of arching roots all seemed to indicate that there the seed germinated on mineral soil.

States. This shrub seems to be restricted, almost without exception, to the old growth stands of the association and is rarely found elsewhere in this region save infrequently in bogs. The apparent inability of leatherwood to endure any but the most mesic conditions greatly limits its present distribution.

Beaked hazelnut, *Corylus cornuta,* the shrub species showing the greatest density in two of the three stands (table X), can hardly be called characteristic of the climax but may be found in almost any type of forest community in northern Wisconsin.

Two species of *Ribes, R. cynosbati* and *R. lacustre* were present in the quadrats with a third species *R. triste* also appearing in the stands although not present in the quadrats. The absence of *R. lacustre* from the Tenderfoot Lake stand cannot be explained by data available. Two other shrubs commonly found in the climax forest, *Cornus alternifolia* and *Viburnum acerifolium,* are present in such low densities that no valid comparisons can be made between stands. *Sambucus pubescens* is distributed widely throughout the northern part of the state in a variety of communities. It occurs in the climax mainly in windfall openings where the light is more intense than under the full canopy.

Rubus idaeus is obviously a species of successional communities invading an area of recent disturbance near the edge of the Tenderfoot Lake stand. It will invade any climax stand which suffers serious disturbance. As has been pointed out by Olmsted and Curtis (1947), seeds of *Rubus* are usually present in the forest floor and are thus in position to take quick possession of an area when conditions become suitable.

The density and frequency of shrub species suggest a rather open forest floor except where sugar maple reproduction has been unusually successful.

When one compares the species present here with lists and data from other stands one of the most obvious omissions is the American yew, *Taxus canadensis.* This is particularly noticeable when the lists from early studies in the Michigan Peninsula are examined since they specify yew as abundant. In 1932 the writer made his first contact with the Laona stand and observed several fairly prominent clumps of *Taxus;* however, during the course of the present study none remained. The apparent explanation is that yew, a favorite food of the white tailed deer (Swift 1946) has been almost completely eliminated in the areas where winter deer pressure is heavy. Although the writer was continually on the alert for this species, the only plant noted during the summer was in an area of sugar maple-hemlock-yellow birch forest bordering directly on a heavily traveled state highway.

TABLE IX. *Density per acre of components of the shrub layer*

	Laona	Tenderfoot Lake	Drummond	Average all stands
Densities per acre†				
Shrub species	1,656	1,612	965	1,439
Tree reproduction‡	23,340	42,150	29,175	31,185
Total of shrub layer	24,996	43,762	20,141	32,624
Maple reproduction	20,362	38,780	26,823	28,588
All other components of the shrub layer	4,634	3,982	3,318	4,036
Percentage of shrub layer composed of sugar maple reproduction	81.5%	90.9%	89%	87.6%

† Density per acre is computed on the basis of total acreage of the 2 by 8 meter quadrats as follows: Laona, 0.138 acres; Tenderfoot Lake, 0.118 acres; Drummond, 0.107 acres; and the average on a total acreage of 0.364 acres.

‡ Tree reproduction includes all tree seedlings and saplings up to one inch d.b.h.

TABLE X. *Density† and frequency‡ data* for shrub species*

Species	Place	0–12"		13–36"		37–72"		All sizes D
		D	F %	D	F %	D	F %	
Dirca palustris	Laona	51	22.9	125	45.7	29	11.4	205
	T. Lake	47	27	67	36	27	10	141
	Drum'd	11	11.1	59	33.3	11	7.4	81
Corylus cornuta	Laona	80	22.9	60	17	31	8.6	171
	T. Lake	183	27	157	30	37	10	380
	Drum'd	37	14.8	100	25.9	18	3.7	155
Ribes cynosbati	Laona	3	2.9	17	5.7	—	—	20
	T. Lake	57	16.7	16	13.5	—	—	73
Ribes lacustre	Laona	131	20	83	25.7	17	5.7	231
	Drum'd	26	11.1	4	3.7	—	—	33
Cornus alternifolia	Laona	—	—	—	—	3	2.9	3
	Drum'd	4	3.7	—	—	—	—	4
Rubus ideaus	T. Lake	17	3.3	27	3.3	—	—	44
Sambucus pubens	Laona	3	2.9	20	14.3	—	—	23
Viburnum acerifolium	Drum'd	37	7.4	74	11.1	—	—	111
Total all species	Laona	268	—	305	—	80	—	654
	T. Lake	304	—	267	—	64	—	637
	Drum'd	114	—	237	—	29	—	382

† Density (D) is given as number per 100 2 by 8 meter quadrats (1,600 sq. meters).
‡ Per cent frequency (F) is given for 2 by 8 meter quadrats.
* Basis for data is as follows: Laona, 35 quadrats; Tenderfoot Lake, 30 quadrats; and Drummond, 27 quadrats.

Of the species consistently present in the shrub layer, *Acer spicatum* is probably the most abundant (excluding sugar maple). *Sambucus pubens* and *Ribes cynosbati* are listed as present in almost every study of the sugar maple-hemlock-yellow birch association, although not in great numbers. *Viburnum acerifolium* and *Cornus alternifolia* are also present in small numbers in many stands from Wisconsin eastward to Maine.

THE HERB LAYER

The time available for this study did not permit a thorough examination of the herbaceous species of the climax. Due to the necessity of studying one stand at a time, none of the three areas received coverage throughout the entire season. The Laona stand had the widest seasonal coverage since it was visited in June, July, August, September, and November. Each of these visits, however, concerned different quadrats so that exact seasonal fluctuations were not recorded. Those species on which data are considered unreliable for comparative purposes as a result of seasonal variations are designated with an asterisk (*) in table XI. Comparison between stands is likewise doubtful for species with low frequency.

The more common species are recognizable during most of the season so that it is possible to get a good picture of the herbaceous composition of the association at almost any time from June to September. Only a small percentage of the ground surface is covered with either herbaceous plants or shrubs. The plants that are present are usually fairly well dispersed, save where a high water table (due to a clay layer close to the surface) and an opening in the crown coincide. At such points many different herbaceous

TABLE XI. *Density† and frequency data‡ for herbaceous species of the sugar maple-hemlock-yellow birch association*

Species	Laona		Tenderfoot Lake		Drummond		Avg. of all stands	
	Density	Freq. %	Density	Freq. %	Density	Freq. %	Density	Freq. %
Maianthemum canadense	594	66.	527	53.4	259	40.8	474	54.4
Dryopteris spinulosa	234	71.5	147	47	37	18.5	52	48
Polygonatum pubescens	94	45.7	93	30	300	59.4	159	44.6
Viola spp.	560	48.6	190	33.3	412	33.3	402	39.2
Grasses spp.*	189	20	107	16.6	937	74.0	382	32.6
Clintonia borealis	189	37	7	6.7	218	55.6	138	32.6
Streptopus roseus var. *longipes*	643	63	40	16.6	11	7.9	261	31.5
Lycopodium obscurum	74	20	273	30	270	44.5	131	30.4
*Arisaema atrorubens**	234	40	47	23.3	30	22.2	113	28.3
Osmorhiza claytoni	169	40	30	13.3	33	7.4	84	21.8
Lycopodium lucidulum	217	28	350	26.7	34	3.7	198	20.6
Galium spp.	77	20	100	23.3	41	18.5	93	20.6
*Trientalis borealis**	49	20	37	26.7	33	14.8	40	20.6
Mitella diphylla	177	31.4	X	X	52	11.1	83	15.2
Aralia nudicaulis	77	20	23	6.7	22	14.8	43	14.2
Carex spp.	49	14.3	30	16.6	37	7.4	39	13
Mitella nuda	89	25.7	X	X	22	7.4	40	12
Mitchella repens	65	14.3	77	6.7	70	18.5	71	10.9
*Circaea alpina**	463	14.3	77	3.3	148	11.1	245	9.8
*Uvularia grandiflora**	100	20	30	6.7	X	X	47	9.8
*Oryzopsis asperifolia**	91	25.7	X	X	—	—	35	9.8
Aster macrophyllus	17	14.3	—	—	15	14.8	109	9.8
Dryopteris Linnaeana	29	2.9	613	16.7	48	7.4	215	8.7
Dryopteris Phegopteris	71	14.3	67	6.7	X	X	48	7.6
Lycopodium complanatum	—	—	3	3.3	48	22.2	15	7.6
Oxalis montana	129	11.4	413	6.7	—	—	184	6.6
Coptis trifolia	100	2.8	100	10	7	7.4	73	6.6
Adiantum pedatum	11	5.7	7	3.3	44	11	20	6.6
Cornus canadensis	11	2.8	640	10	—	—	213	4.4
Lycopodium annotinum	—	—	27	10	4	3.7	10	4.4
Uvularia sessilifolia	71	2.8	10	3.3	18	7.4	36	4.4
Caulophyllum thalictroides	9	5.7	7	3.3	7	3.7	8	4.4
Pyrola elliptica	20	2.8	—	—	33	7.4	17	3.3
*Schizachne purpurascens**	14	8.6	X	X	—	—	5	3.3
Minor species**	51	—	213	—	37	—	100	—
Number of minor species	4	—	6	—	4	—	14	—
All species	4,967	—	4,285	—	3,197	—	4,183	—
Number of species represented in quadrats	36	—	35	—	32	—	48	—
Number of species represented in stand but not in quadrats	18	—	11	—	10	—	—	—

† Density is expressed here as the number of upright stems per 100 quadrats, *i.e.*, per 400 square meters. The density figure does not of course represent the actual number of individual stalks in clonal species such as *Maianthemum canadense.*

‡ Data were obtained from 1 × 4 meter quadrats distributed as follows: Laona, 35 quadrats; Tenderfoot Lake, 30 quadrats; Drummond, 27 quadrats.

* Some of the variation between stands results from the differences in the time of the season at which the stands were examined. See text.

** A species represented in only one herb quadrat in one stand.

X indicates that the species is present in the stand but not in the herb quadrats. Other species were observed in one or more of the stands but were not recorded in the herb quadrats. These and minor species (see double asterisk above) are listed as follows: *Actea pachypoda, Actea rubra, Allium tricoccum, Anemone quinquefolia, Botrychium virginianum, Circaea latifolia, Claytonia caroliniana, Corallorrhiza maculata, Cystopteris fragilis, Dicentra cucullaria, Frageria vesca, Gaultheria procumbens, Geum canadense, Goodyera repens, Hamamelis virginiana, Hepatica acutiloba, Impatiens biflora, Linnaea borealis, Lycopus uniflora, Monotropa uniflora, Onoclea sensibilis, Osmunda claytoniana, Phyrma leptostachya, Pteretis nodulosa, Ribes triste, Rubus* spp., *Sanguinaria canadensis, Scutellaria lateriflora, Smilacina racemosa, Smilax hispida, Solidago latifolia, Trillium cernuum, Trillium grandiflorum.*

species congregate and grow vigorously.

Space does not permit a detailed discussion of each of the herbaceous species which were found in the quadrats. Density and frequency are given in table XI, arranged in order of decreasing frequency.

The more common species listed both in point of view of density and frequency are also found, often in greater numbers, in various subclimax communities of the northern hardwood forest. *Maianthemum canadense, Clintonia borealis,* and *Trientalis borealis* all serve as examples. They have been listed by other workers and observed by the writer in a variety of different communities including aspen stands, pine stands and tamarack bogs. The presence of such species of herbs in a variety of successional communities, often seemingly out of place, is frequently a result of catastrophe in an earlier climax stand. *Actea rubra* and *Caulophyllum thalictroides* growing in an aspen-pin cherry thicket are obviously survivors from a previous community. On the other hand, *Clintonia borealis* and *Trientalis americana* in a bog habitat are recognized as legitimate members of the bog sere.

From a study such as this one it is extremely difficult to pick out with certainty herbaceous species which are confined only or chiefly to the single association studied. Species lists with frequency and density data from many different types of communities in the same general region would be necessary.

Perusal of lists from earlier studies supplemented by notes made by the writer make possible the proposal of a tentative list of the typical herbaceous species of the sugar maple-hemlock-yellow birch association. The list that follows applies only to the northern portion of the Lake States.

Adiantum pedatum
Dryopteris spinulosa
Lycopodium lucidulum
Lycopodium obscurum
Oryzopsis asperifolia
Arisaema atrorubens
Uvularia grandiflora
Clintonia borealis
Maianthenum canadense
Streptopus roseus var. *longipes*
Polygonatum pubescens
Coptis trifolia
Caulophyllum thalictroides
Mitella diphylla
Mitella nuda
Oxalis montana
Osmorhiza claytoni
Viola spp.

There are other species typically found in the climax but those listed above are the ones which are either abundant in or always present in stands of this association. It will be noted that many of these species are also typical of the beech-maple association, of the boreal forest, and of the maple-basswood "bigwoods" of Minnesota.

Summary

Data gathered in three "virgin" or undisturbed stands of the northern hardwood forest in northern Wisconsin show that although there is considerable variation between communities there is sufficient homogenicity to establish a typical grouping of species, the sugar maple-hemlock-yellow birch association, which may be considered as the normal climax forest for northern Wisconsin. This association is found on relatively fertile and well drained loamy soils and is replaced by an edaphic climax of pine species on the sandy soils.

The composition of the sugar maple-hemlock-yellow birch association, determined on the basis of dominance (taking an average of the three stands) is as follows: sugar maple (*Acer saccharum*) 28 per cent, hemlock (*Tsuga canadensis*) 23.8 per cent, yellow birch (*Betula lutea*) 24.9 per cent, basswood (*Tilia americana*) 13.8 per cent, white pine (*Pinus strobus*) 4.8 per cent, American elm (*Ulmus americana*) 2 per cent, with the remaining 3 per cent made up of assorted minor species including ironwood (*Ostrya virginiana*), blue beech (*Carpinus caroliniana*), white ash (*Fraxinus ameri-*

cana), and balsam fir (*Abies balsamea*). Typical shrubs of the climax are *Corylus cornuta, Dirca palustris,* and *Ribes cynosbati* while the most common herbaceous species include *Maianthemum canadense, Dryopteris spinulosa, Polygonatum pubescens, Clintonia borealis, Lycopodium obscurum,* and *Viola* spp.

The composition of every stand shifts continuously as a result of the natural vicissitudes to which it is subjected. Natural catastrophes are to be considered a normal and common occurrence in the life of the forest and take the form of windfall, fire, ice storm, or epidemic disease. The ultimate result of each individual occurrence upon composition depends not only upon environmental conditions preceding the event but also upon those following since both the availability of seed, germination of that seed, and survival and growth of the resultant seedlings are concerned.

The role of white pine as an indicator of stand history is discussed briefly as is the history of the three stands. The Laona area seems to have suffered little disturbance over the past 400 years and appears to have reached a state of equilibrium or very slow change. The Tenderfoot Lake stand shows some evidence of disturbance approximately 200 years ago although the stand was not destroyed at the time but rather small island-like patches were affected, presumably by heavy windthrow. The Drummond stand also shows evidence of disturbance about 200 years ago, in this case a major although not complete change involving perhaps both wind and fire. Its nearness to the Bayfield County pineries is postulated as explaining the greater likelihood of fire.

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INTERSPECIES COMPETITION AND ITS PROBABLE INFLUENCE UPON THE VERTICAL DISTRIBUTION OF APPALACHIAN SALAMANDERS OF THE GENUS PLETHODON [1]

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Competition lies at the foundation of evolution by natural selection; it is assumed to be of universal occurrence within species, and almost as frequent between distinct species. The subject of interspecies competition has recently received an excellent review by Crombie (1947), and no attempt has been made here to give a complete bibliography. The complexity of the situation in nature makes even the description of natural cases of interspecies competition difficult and therefore rare, and analysis of such cases is even more hazardous. Notable successful examples are Beauchamp and Ullyott (1932) for freshwater triclads, and Lack (1945) for birds. The laboratory experiments of Gause (1934), Crombie (1945), Park (1948), and others have yielded valuable information on the problem, but even in such oversimplified cases, little has been discovered concerning the mechanisms by which successful species achieve the demise of their competitors.

There are certain obvious differences between interspecies and intraspecies competition. The former has frequently been demonstrated to lead to the elimination of one competitor when two species are confined within a limited space, all parts of which are accessible to each, and given a source of food which each can utilize. A deviation from strict adherence to these conditions may permit the two species to co-exist (*cf.* Crombie 1945), and the natural environment usually offers a sufficient variety of refuges and of food so that the result of interspecies competition must frequently be shifts to food sources or habitats in which competition is of reduced intensity. Intraspecies competition may lead to evolution, emigration, changes in population size, etc. It is assumed that individuals of a species are in competition with one another when they inhabit the same locality. The corollary of this trite statement is that members of interbreeding populations (subspecies) avoid interspecies competition where they come in contact with one another. The point is raised because, in studying competition between species, it is important to be as certain as possible that there is no interbreeding, as this would transfer the problem to an intraspecies situation. The question will arise only among forms with allopatric but contiguous distributions, or among those sympatrically distributed ones that show ecological segregation within the general area covered by both species (or subspecies, see Fitch 1940).

The present paper is concerned with interspecies competition, and it seems advisable to examine the criteria by which this can be demonstrated in nature. A number of these criteria have been used, consciously or unconsciously, by various authors. They may be enumerated as follows:

1. Closely related species are in competition when they occur together. This is based on the assumption that taxonomic affinity and ecological requirements are closely correlated, an assumption that is undoubtedly correct in general. The taxonomic category most frequently used here is the genus (Elton 1946; see Williams 1947 for an opposing view). There

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are objections to this use of the genus, whether the evidence is interpreted as indicating competition or not. There are the assumptions that we know what a genus is, and that genera are the same in different groups of animals. Both assumptions are patently invalid, as the genus varies in inclusiveness from group to group, depending most frequently upon amount of taxonomic work that has been done. Thus, *Plethodon glutinosus* and *P. cinereus* would undoubtedly be placed in different genera, if the general procedures of ornithology were followed by herpetologists. Grobman (1944) has suggested splitting the genus, and if this were done, the common presence of the two species over much of the eastern United States might be interpreted quite differently, as far as possible competitive relationships are concerned. Thus, a trend toward splitting or lumping in several groups could change the data and hence could change one's views.

Even in cases where the taxonomic relationship is really close, one must be cautious about assuming competition, as the occurrence of sibling species attests. On the contrary, the hypothesis might be advanced that the common presence of two closely related species over a wide area is evidence of the lack of competition between them (Crombie 1947).

2. Species having one or more ecological requirements in common are in competition. There is nothing theoretically wrong with this criterion. However, it cannot be assumed that two species are actually competing for something simply because they both need it. The vast majority of organisms use free oxygen, but only in a few situations could there be any competition for it. In short, the requirement must be in critical supply before there is competition. By critical is meant that if one species is successful in obtaining the requirement, a competing species is more or less prevented from obtaining it. The example of the starling taking available nesting sites to the partial exclusion of native birds is to the point. It is rarely so easy to conclude that an ecological requirement is in critical supply, even though it may be rare. Hutchinson (1944) presented evidence that in small eutrophic lakes all inorganic nutrient substances, except phosphorus and combined nitrogen, are present in great excess. He suggested that the diatom *Fragilaria crotonensis* and the blue-green alga *Anabaena circinalis* were in competition for phosphate; the former was favored by high concentrations of nitrate, the latter by low.

3. Species having mutually exclusive ranges or stations are in competition at their zones of contact. Universally applied, this criterion has at least one serious objection. This is that some environmental factor other than competition is restricting the two species to their distinct ranges. Such factors might be the climate operating directly through temperature, rainfall, etc., or indirectely through the vegetation. Soil differences might also have this effect. Most of such factors should be readily apparent through field studies. If the boundary between the ranges of a pair of animal species does not coincide with vegetational distribution, the latter may be ruled out as a factor. Moreover, in cases where the physical environment alone is operating, there should be a gradual change from a preponderance of one species to a preponderance of the other. This situation would involve a relatively broad zone over which both species are present. Such a situation has been described in the salamander genus *Desmognathus* (Hairston 1949). Strict mutual exclusion, in the absence of intergradation or sharply delimited envnronment, would thus appear to be a valid criterion of competition, and one that is practicable for use in field studies. A classic example of its use is the work of Beauchamp and Ullyott (1932), who found that *Planaria montenegrina* was restricted to water colder than 13–14° C., and *P. gonocephala* to water warmer than this temperature, when both species were pres-

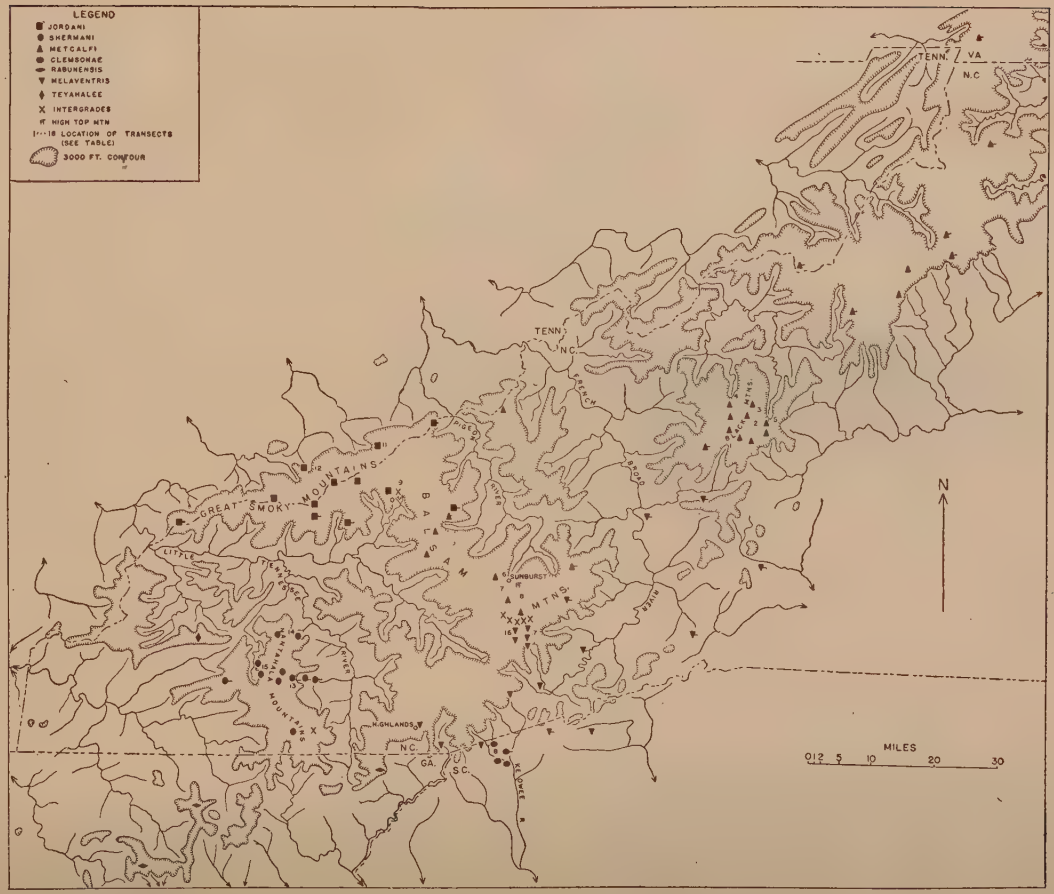

FIG. 1. Map of the southern Appalachians, showing distribution of the subspecies of *Plethodon jordani*. A short line attached to a symbol indicates a literature record, some of which were omitted when encompassed by the records shown. Map adapted from U. S. Coast and Geodetic Survey Sectional Aeronautical Charts R–8 and S–8 (Charlotte and Winston-Salem), 1936.

ent in the same stream. Either species could occur beyond this limit in streams where they occurred alone.

The present paper is a description of the vertical distribution of two species of terrestrial salamanders, *Plethodon jordani* and *P. glutinosus*. The former is a polytypic species represented by seven subspecies, all restricted to various parts of the southern Appalachians (Hairston 1950). Their distribution is indicated in figure 1. *Plethodon glutinosus* is widespread over the eastern United States, and is fairly constant morphologically throughout most of this area, although there are minor variations (Bailey 1937; Grobman 1944). In the southern Appalachians, the two species are in contact at many places, but the relationship is by no means the same everywhere. The remarkably sharp altitudinal separation of *P. glutinosus* from *P. jordani metcalfi* in the Black Mountains has been described (Hairston 1949); this discovery prompted the study to be described.

Methods

During the summer of 1949, the author was able to make field investigations of the vertical distribution of *P. glutinosus* and the following subspecies of *P. jordani: metcalfi* near its type locality, Sunburst, on the north side of the Balsam Mountains, *melaventris* on the south side Balsams, *jordani* at several locations in the Great Smoky Mountains, and *shermani* at several locations in the Nantahala Mountains. Previously, observations had been made on the local distribution of *P. j. clemsonae* and *P. glutinosus*. Thus, five of the seven subspecies of *jordani* are represented in this study; no vertical distribution data are available for *rabunensis* and *teyahalee*.

The method used was to select a situation that offered a continuous slope of at least 1500 vertical feet, facing in one direction. A transect was then made, collections or observations being taken at frequent intervals, usually not farther apart than 100 feet vertically. The zone of potential or actual overlap was examined especially carefully. Elevations were determined with an aneroid altimeter (Taylor No. 2075D), which was set at a benchmark at the beginning of each day, and checked at the end of the day. The maximum error was found to be 25–50 ft.

Observations

The extremes of observed vertical distribution for both species in each transect are given in table I. The details are represented graphically in figure 2, where each symbol represents one specimen. The absence of desirable records does not mean that the locations in question were not searched for *Plethodon;* for example, the 975-ft. vertical gap between species in the transect of the Left Prong, West Fork of Pigeon River was searched thoroughly for ten full days without success, and four transects were abandoned because the specimens found were too few and scattered to yield satisfactory results. Deforestation, either through timbering or fire, is thought to be the cause for present absence of either species of *Plethodon*. The data presented leave no doubt as to the general situation. *P. glutinosus* is sharply separated vertically from three subspecies of *P. jordani: metcalfi, jordani,* and *shermani*.[2] The maximum observed overlap in any transect involving these three subspecies is 200 vertical feet, and even this small amount of overlap was found in only two of fifteen transects.

The variable elevation of the narrow zone of contact between the two species indicates that climate determines where this zone will fall. Thus, the two species are in contact at lower elevations on

[2] The author admits the possibility of interbreeding between *glutinosus* and *shermani,* but does not believe that it occurs; no claims of intergradation have ever been made between *glutinosus* and any other subspecies of *jordani* (see Bishop 1941b; Grobman 1944; Hairston and Pope 1948; Hairston 1950).

TABLE I. *Extremes of vertical distribution (in feet) of five subspecies of* Plethodon jordani, *as compared with* P. glutinosus *in eighteen transects in the southern Appalachians*

Subspecies of *jordani*	*metcalfi*								Inter-grades	*jordani*			*shermani*			*melaventris*		*clem-sonae*
Area	Black Mountains					Balsam Mountains			Great Smoky Mountains				Nantahala Mountains			Balsam Mountains		Jocassee
Average annual rainfall	74.49 in.					61.87 in.				81.71 in.			65.69 in.			61.87 in.		?
*Transect number (see map)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Slope faces approximately	S	E	E	N	N	E	N	N	W	S	W	N	E	E	NW	S	S	E
Highest *jordani*	6,350	6,550	5,500	6,350	5,000	5,100	6,100	5,700	4,400	3,800	4,250	5,100	4,100	4,000	4,100	5,550	5,300	1,350
Lowest *jordani*	5,300	4,800	3,350	3,300	3,000	4,750	3,750	4,525	3,940	3,425	3,100	2,850	2,500	2,800	2,850	3,400	2,350	800
Highest *glutinosus*	4,750	3,600	3,550	3,100	3,000	4,900	3,800	3,550	3,950	3,460	2,950	2,850	2,300	2,750	3,050	5,350	4,500	2,200
Lowest *glutinosus*	2,400	3,000	2,700	2,700	2,700	3,100	3,100	3,100	3,240	3,240	2,950	1,700	2,300	2,125	2,260	3,400	3,000	850
Vertical overlap			200		0	150	50		10	35		0			200	1,950	1,500	550

* Transects are located as follows: *1*, North Fork of Swannanoa River; *2*, Little Mountain and Mount Mitchell; *3*, Middle Creek; *4*, Cane River; *5*, Neal's Creek and South Toe River; *6*, Right Prong, West Fork of Pigeon River; *7*, Middle Prong, West Fork of Pigeon River; *8*, Left Prong, West Fork of Pigeon River; *9*, West Slope of Hyatt Ridge; *10*, Raven Fork of Oconaluftee River; *11*, Ramsay Prong of Little Pigeon River; *12*, Road Prong and West Fork of Little Pigeon River; *13*, Wayah Creek; *14*, Rhinehart Creek; *15*, Nantahala River; *16*, Tennessee Ridge; *17*, Courthouse Creek; *18*, Whitewater River.

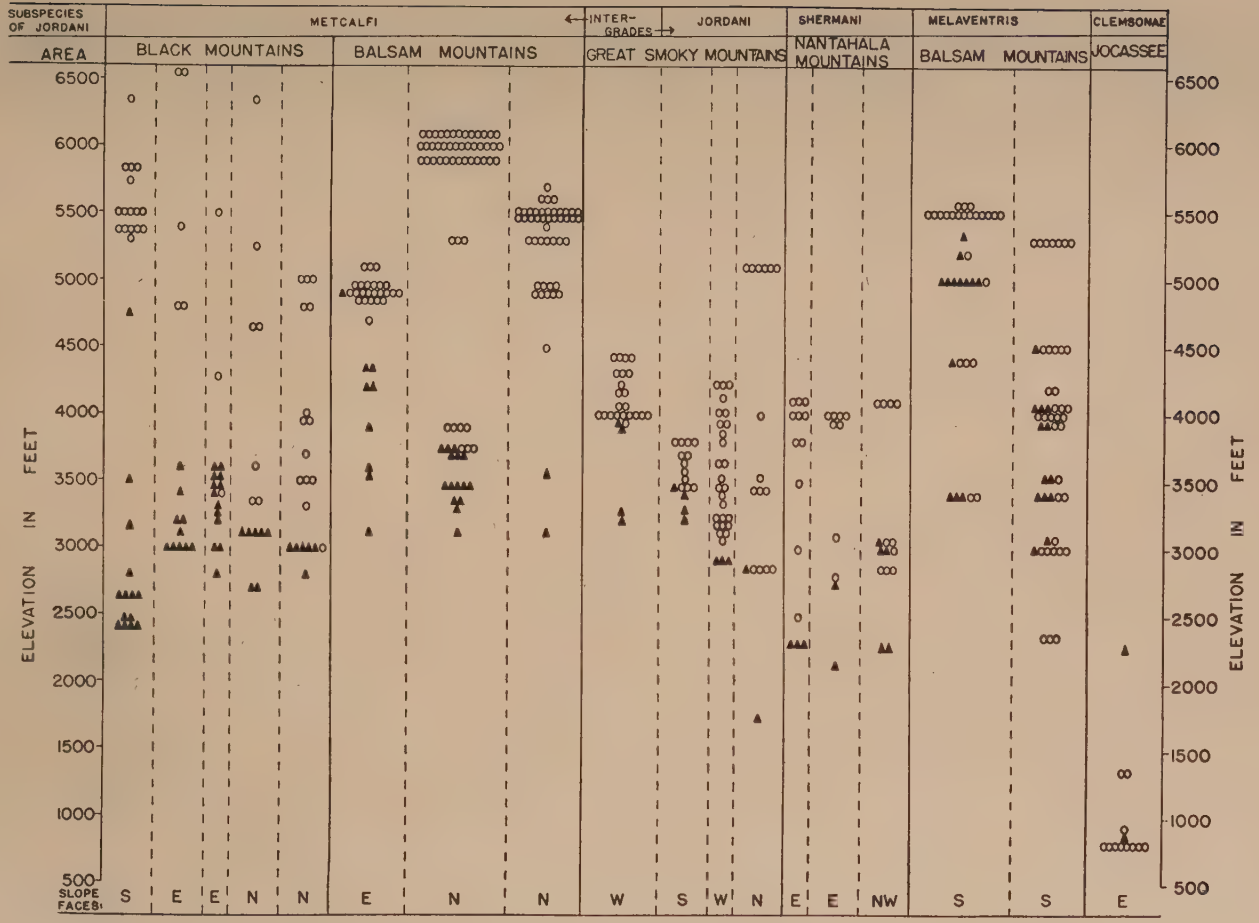

FIG. 2. The vertical distribution of *Plethodon glutinosus* compared with five subspecies of *P. jordani.* Triangles represent *glutinosus,* circles the subspecies of *jordani.* Each symbol represents one specimen.

north-facing slopes than on south-facing ones, and east- and west-facing slopes are intermediate. This climatic influence is also evident in comparing the Black and Balsam Mountains transects involving *P. j. metcalfi.* The zone occurs at higher elevations in the Balsams, which lie about 55 miles southwest of the Blacks, and get less rain (see table I).

There is only one major, clear-cut vegetational change on the slopes of these mountains. This is the shift from deciduous forest to spruce-fir. The rather sharp line delimiting the two forest types occurs at a considerably higher elevation than the line separating the two species of salamanders. In every transect except one, the salamanders meet well within the deciduous forest. The exception is the south-facing slope in the Black Mountains, where the lines between forest types and salamander species coincide. Moreover, there is no spruce-fir forest in the Nantahala Mountains. There is no evidence that the vegetation influences the vertical distribution of either *Plethodon jordani* or *P. glutinosus.* The situation is quite different from most of the altitudinal differences reported for species of Guatemalan Plethodontids by Schmidt (1936).

As the figure indicates, *glutinosus* meets *jordani, shermani,* and *metcalfi* at different elevations, even on slopes that face in the same general direction. This variation between the three subspecies of *jordani* in their relations with *glutinosus* may be partly or entirely due to genetic differences. The evidence against this view consists of climatic data for their separate ranges, as the average annual rainfall differs by as much as 16 inches between the areas involved (table I). The evidence favoring the influence of genetic differences is to be seen in the entirely different ecological relationship between *P. glutinosus* and the two remaining subspecies of *P. jordani: melaventris* and *clemsonae* (table I and fig. 2). These two subspecies are completely overlapped vertically by *glutinosus.* There is some evidence of slight differences in habitat preference between *glutinosus* and *melaventris;* the former appears to be the more abundant in drier situations (Tennessee Ridge), the latter in moist coves (near Courthouse Creek). Both species are found in both places, however, and there is no evidence of ecologic segregation, even on a microhabitat basis. Similar remarks would be applicable to the situation between *glutinosus* and *clemsonae.* In other parts of the range of *melaventris,* the discrepancy in numbers between it and *glutinosus* may be more marked. This is especially true at Highlands, N. C., where *melaventris* is extraordinarily abundant, but *glutinosus* is rare (Pope 1928, and personal observation).

As something of an addendum to the data presented, these facts should be stated: first, *Plethodon glutinosus* ranges to sea level, and hence its indicated vertical range could be extended downwards in every transect without straining accuracy. The author feels that it is best to present on the chart only the data that he has acquired. Second, *glutinosus* ranges upwards to much higher levels on ridges that do not present a large enough high-altitiude area to maintain a population of *jordani.* Such a situation is found on High Top Mountain, directly across the West Fork of the Pigeon River from Sunburst. This mountain, over 5,100 feet in height, is small on top, and *glutinosus* was found nearly to its summit. No *metcalfi* was present. Moreover, where *glutinosus* is in contact with *melaventris,* it reaches an elevation of 5,340 feet on Tennessee Ridge. This is a south-facing situation, though, and is not as convincing as the presence of the low-altitude salamander on High Top, which faces west and north. There would thus seem to be no climatic barrier to the occupancy by *glutinosus* of the entire territory covered by *jordani.* Additional evidence for this statement is seen in the geographic range of *glutinosus,* which is found as far north as Lake Ontario

(Bishop 1941a). Third, given slopes facing in the same direction, the line between the two species occurs at higher elevations on the dry ridges than in the moist coves. On the ridge adjacent to the Middle Creek transect in the Black Mountains, *glutinosus* was found at an elevation of 3,850 feet, 250 feet higher than in the cove.

Discussion

Possible factors in competition

For the reasons outlined at the beginning of the paper, it is concluded that severe competition is responsible for the sharply delimited vertical distribution described. With forest type ruled out as a controlling factor, no other feature of the common environment of the two species changes with sufficient abruptness to produce the observed effect. It is evident that the local climate determines the elevation at which one species gives way to the other. Climatic factors probably limit the downward distribution of *Plethodon j. jordani, P. j. metcalfi,* and *P. j. shermani.* The reverse postulate that the upward distribution of *P. glutinosus* is limited by climate is not tenable because this species ranges to the tops of mountains not inhabited by one of the above three subspecies of *jordani.* The conclusion is that *jordani, shermani,* and *metcalfi* in some way prevent *glutinosus* from entering their ranges. It is useless to speculate upon the nature of the mechanism involved without considerable information concerning the details of life-history and ecologic requirements of both species, and this information is not available at present. Perhaps the most fruitful line of attack would be a comparison of all of the subspecies of *jordani* in this regard. Since at least two of these (*melaventris* and *clemsonae*) have different distributional relations with *glutinosus,* differences between them and the other subspecies should indicate the critical requirements about which competition is centered. At the same time, one should not ignore the possibility that *metcalfi, jordani,* and *shermani* have some specific mechanism for preventing *glutinosus* from invading their environment. These three subspecies, in the order just named, are the most specialized of the subspecies of *jordani* (Hairston and Pope 1948), and could conceivably have advanced beyond *clemsonae* and *melaventris* in this regard.

Intraspecies variation in competitive resistance

If the facts are correctly interpreted, this is the first case known to the author of geographic variation in competitive resistance to another species. Such variations in physiology and ecologic requirements generally are common (Mayr 1942; Lack 1947), one of the best-known studies on amphibians being Moore's work on *Rana pipiens* (Moore 1949). It is thus not surprising that one such variable species might be relatively tolerant to another in part of its range, and in sharp competition with it elsewhere. The assumption here is that *P. glutinosus* is a satisfactory "yardstick" against which the subspecies of *jordani* can be compared. It is possible that *glutinosus* itself is variable in ecology in the areas concerned, but this would simply transfer the postulated phenomenon to another species. It seems better to assume that the morphologically variable *jordani* is the species that varies in competitive resistance. This assumption is given increased validity by the observation that both *P. j. melaventris* and *P. j. clemsonae* are found at much lower elevations than are the other three subspecies studied. The lowest recorded limits for the five subspecies treated herein are: *jordani,* 2850 ft.; *metcalfi,* 3,000 ft.; *shermani,* 2,300 ft.; *melaventris,* 1,200 ft.; and *clemsonae,* 800 ft. Moreover, this difference in lower altitudinal limit is reinforced by the fact that *melaventris* and *clemsonae* are also found farther south than any of the other three subspecies (see map, fig. 1).

Summary

1. The vertical distribution of *Plethodon glutinosus* and *P. jordani,* two species of salamanders inhabiting the Southern Appalachians, was studied by means of eighteen transects. These transects were made in the ranges of five of the seven subspecies of *jordani: jordani, shermani, metcalfi, clemsonae,* and *melaventris.*

2. *P. glutinosus* is sharply separated altitudinally from the first three, the maximum observed overlap being 200 feet vertically. The elevation at which one species gives way to the other varies with the direction in which the slope faces, and to some extent with geographic location. This indicates that the local climate controls the elevation at which the two species meet.

3. As this zone of contact occurs within the deciduous forest, vegetation seems not to determine the ranges of the salamanders. It is concluded that interspecies competition is responsible for the abrupt vertical limits of the two species.

4. The two remaining subspecies of *P. jordani, clemsonae* and *melaventris,* are completely overlapped by *P. glutinosus,* thus differing markedly from the others in competitive resistance to this species. The author believes this to be the first recorded case of geographic variation in competitive resistance between two distinct species.

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THE RELATION BETWEEN CLASSIFYING AND MAPPING VEGETATION

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The demand for vegetation maps is becoming increasingly emphatic. As a result, a growing number of such maps is becoming available but their quality varies within wide limits. These qualitative differences become more critical as the maps find a wider application.

One of the difficulties in discussing the relation between classifying and mapping vegetation is the meaning of the term vegetation. According to Webster's dictionary, vegetation is the sum of vegetable life, but many authors considerably reduce this comprehensiveness, each according to his own ways of thinking. A valuable discussion of vegetation and related terms was given by Egler (1942).

Then there is the enigmatic "natural vegetation." There are now few areas on the globe where man has not affected the vegetation in some fashion; nevertheless, there is in existence today a considerable number of natural vegetation maps. This implies that we can go back in history to the time when man did not appreciably interfere in a well balanced climax vegetation. Important areas for which such maps exist, especially in Europe, have been settled for so long that it is not at all certain that a reconstruction of the vegetation as it existed several millennia ago is really possible. But granted that it is possible, does it not result in a historical map? For we have learned that the vegetation of an area can change considerably within a few centuries, so that the postulated original natural vegetation is really dated and may or may not at all apply to our own times.

One can go one step further and ask what is "natural" vegetation? Is freedom from human interference enough? The investigators of the Prairie have found that the large bison herds affected the floristic composition of the Prairie, and tall grass species would have grown "naturally" farther west than they did, had it not been for the bison. Was the Prairie then "unnatural"? If so, when was it natural?

These few remarks are enough to indicate that alone the interpretation of the term vegetation must lead to basic variations in both classifying and mapping vegetation. Many authors have therefore returned to the dictionary definition and classify and map "the sum of vegetable life," concerning themselves with what actually exists at the time of their investigation.

Every map that shows differences of vegetation implies a classification and one might argue that every vegetation map is an application of the classification which a particular author happens to choose. This leads to the conclusion that the relation of classifying and mapping vegetation is that of a sequence in which the first item (classification) is arrived at more or less arbitrarily, whereas the second item (vegetation map) expresses the first one cartographically. This conclusion is correct only in part.

A vegetation map presupposes that a number of vegetation categories can be established. These categories can be arrived at in two ways, both of which have been used frequently. One of these is to view the vegetation of the earth as a whole and consider a variety of methods to divide this total into meaningful parts which may then be subdivided repeatedly until one arrives at units so small that further division becomes undesirable. The result of this process is a classification of vegetation. A considerable number of such classifications has been developed. But the marvelous variety of forms which plant life assumes on all continents has been a major stumbling block

to the development of a simple and universally applicable classification, and the problem of classifying vegetation remains an unending one.

Many scholars have therefore taken to the field and proceed on the basis of direct observation: one sets down on a map what one sees and thus accumulates data which can be sorted and organized. Because mapping implies observation, this other way has been used in the case of many vegetation maps. This *a posteriori* mode differs fundamentally from the first method by its direct approach and freedom from preconceived systems, at least theoretically. One maps first, and classifies later. But most authors reveal the powerful influence that existing classifications can exert. The post-mapping classifications show in most instances a close affinity to the *a priori* classifications, more or less modified as local circumstances and the author's originality dictate.

Parenthetically, a word about the distinction between *a priori* and *a posteriori* approaches to mapping may be necessary. There is no question about *a priori* classifications. But may one not assume on logical grounds that all classifications are *a priori?* Even though one may not decide in advance what classification to employ, does not the use of categories while mapping the vegetation imply that some classification has already been established? However, in the case of vegetation maps, the difference is not only real but significant. An *a posteriori* classification evolves from a set of terms, which was assembled while mapping and often newly coined at that time. This is not yet a classification, and only when these terms have been arranged appropriately to permit the distinction of classes, each of which has its significant divisions, can one begin to speak of a classification. For a set of terms and a classification are not at all the same.

As an illustration, one may compare the map of Northwest Montpellier by Braun-Blanquet (1947) who uses an *a priori* classification with the Patuxent map (U. S. D. I. 1945) where an *a posteriori* classification is employed. The difference is obvious. Braun-Blanquet's classification was devised long before the map was drawn, in fact, quite irrespective of the map. The classification was there first; it can be used anywhere (within limits) and that a map of Montpellier was drawn is almost incidental. Not so the Patuxent map. No classification of vegetation was established before the map was planned. The vegetation was the given starting point, and then, while mapping it or afterwards, the various categories were given names. This eventually resulted in a distinctly *a posteriori* classification. Placing the two maps side by side, clearly illustrates the difference between the two approaches. The *a priori* classifications usually have a distinct advantage: they are world-wide in scope and more or less systematic, *i.e.,* they are based on one or more defined ideas which are then applied throughout the classification to the exclusion of other ideas. In contrast, most *a posteriori* classifications are characterized by features which limit their usefulness areally and by being less systematic: ideas are taken more or less indiscriminately from various other systems and used as they fit into the local scene. This method *can* be highly descriptive but is usually less useful and renders comparative studies very difficult if not impossible, especially when the regions to be compared are widely separated.

It now becomes necessary to introduce a new aspect into the discussion: the purpose of the map. This purpose controls both classification and field observation to a considerable degree and more or less complicates the matter. The effect of a given purpose is often to emphasize certain features of the vegetation while neglecting or even ignoring others according to their relation to the purpose of the map. The purpose, in turn, links the map with the people who are to use it. Bot-

anists are by no means the only ones interested in vegetation maps and whether or not their actual number is increasing, their proportion among those who use vegetation maps is rapidly declining to a small percentage. On the other hand, there are growing numbers of geographers, zoologists, geologists, plant and animal ecologists, pedologists, and an ever increasing multitude of people concerned with land planning, forestry, agriculture, conservation, climatology, communications, investments, and military matters who are discovering the practical value of vegetation maps as applied to their respective fields. The nature of the purpose controls the comprehensiveness of the vegetation map and often restricts its usefulness.

The classification of vegetation, the author's observations and the purpose of the map combine to control the character of the map. Observation and purpose are less debatable: the former can be checked in the field as to accuracy, whereas the latter is predetermined. On the other hand, whether an author develops his own classification or employs one already in existence, with or without modifications, the result is always open to criticism, no matter how carefully devised, how clearly defined or how well proved. As a result, vegetation maps show a great variety of classifications, among which the older ones sooner or later give way to more modern ones or are revised to meet the changing standards.

It is perhaps astonishing that the basic ideas underlying all classifications of vegetation as we find them on maps are very few in number. The complexity of the world's vegetation, the great variety of purposes, the incalculable personal elements, the problems of definition, the historical and environmental aspects, all would lead one to believe that classifications can be counted in scores. A closer examination reveals, however, that all vegetation maps are based on classifications which rest on four basic concepts only. The many vegetation maps are only variations of the same themes and the great variety among the existing maps is due to the fact that these themes can be employed singly or in combination and the combinations are almost infinite in number. The four basic themes are: 1. regional, 2. physiognomic, 3. floristic, and 4. ecological. A classification strictly limited to one such concept can be clearer and simpler than a classification based on a combination of concepts. If, on the other hand, more than one basic concept is introduced, the scope of the map can be extended enormously.

The Regional Approach

The differentiation of vegetation into regional units is relatively rare. One does indeed speak of the vegetation of the United States or of Siam, but from a point of view of mapping such an approach is not meaningful.

Somewhat more realistic is the areal division of vegetation within a specified region. In the United States, the southeastern vegetation, the Californian vegetation, and others bear definite connotations, whereas terms such as coastal or mountain vegetation are not purely regional; they imply certain environmental aspects in addition to location and are useful only in relatively small areas and when regional and ecological aspects are to be combined.

A better known application of the regional aspect is found in its combination with physiognomy. Tundra, Taiga, Prairie, Pampa, and many other terms refer to the vegetation of distinct regions where the vegetation bears some definite physiognomic features. Where these features change the region ends. These terms arose spontaneously and are essentially non-technical. Because they usually refer to very distinct vegetative units, however, they have become accepted more and more among scientists. The number of these terms is large (cf. Küchler 1947b) and the better known ones are commonly

found on vegetation maps of the world or of individual continents.

One of the best known (among biogeographers) uses of the regional approach is in its combination with taxonomy. The neotropic realm, the Malagassy region, the Atlantic province, the Macaronesian sector, etc., are based on ideas that go back to Wallace (1876) and beyond. In Europe and parts of Africa these regions have been mapped in great detail, which permits a considerable subdivision of the areas. One need only view the beautiful map of France by Gaussen (1945a) or Trochain's (1940) investigations in Senegal to see how far this work has advanced. In this country an attempt to map the United States on a regional biological basis was published by Dice (1943). Generally speaking, these are not vegetation maps *sensu stricto;* they rather indicate the areal affinities of the flora. However, for the interpretation of the vegetation, such maps are of great value.

The Physiognomic Approach

From the very beginning of the history of plant geography, the appearance of plants has attracted the attention of the investigators (Humboldt 1807) but it was almost a century later before Schimper (1898) put physiognomy on a sounder basis. His monumental work was revised and brought up to date by von Faber (Schimper-von Faber 1935). Others have formulated and used physiognomic classifications, especially in the course of the last three decades. This resurgence of physiognomy may at first be astonishing. Fine and very detailed vegetation maps have been published in Europe for years and many of them show a very advanced standard in every respect. But is physiognomy not a rather primitive method, to be used at best in an unexplored region? It is becoming increasingly evident that physiognomy offers a means of mapping vegetation which is far more valuable than once anticipated. Under the powerful impetus given by Chipp (1926), physiognomy was once again pushed into the foreground and is now used increasingly. Salisbury (1931) strongly promoted it and Champion (1936) used it successfully in India, Beard (1944) in the American tropics, while Burtt Davy (1938) sought to make his approach applicable throughout the tropics. His work was closely followed by that of Richards, Tansley and Watt (1940). Gillman (1949) produced an excellent map of the physiognomy of vegetation of Tanganyika.

Proponents of the physiognomic method agree that the vegetation must be recorded primarily as vegetation and only by its own features. This rules out any floristic considerations and any environmental correlations. It is not denied that the floristic composition and the ecological aspects are very important in the study of vegetation, but they become objects of study *after* the physiognomy has been established. The life forms, the structure of vegetation, the plant community, are the primary target.

"Physiognomy is the most important of the features to be defined in describing a plant community" (Salisbury 1931). Indeed, it is physiognomy which establishes the structure of vegetation and thus implies an important indicator value. And it was again Salisbury (1931) who emphasized very justly the fundamental need for comparative studies of vegetation and the significance of physiognomy in such investigations. Beard (1944) even goes so far as to say: "The physiognomic basis of classification meets all the essential requirements for the treatment of tropical formations. First, structure and life forms are capable of exact measurement and record in the field, and secondly, on the basis of actual types so recorded, structure and life form of any desired formation can be mathematically defined." The important conclusions to which a clear presentation of the physiognomy of vegetation may lead, the value of this approach for comparative studies, and the relative ease with which the perti-

nent data can be compiled, all help to place physiognomy ahead of other investigations in the study of vegetation. Furthermore, the physiognomic method enormously extends the use of vegetation maps as it does not presuppose a taxonomic knowledge of the vegetation. It is therefore not astonishing that physiognomy is increasing in popularity. On the other hand, the physiognomic description can only be a beginning, perhaps the safest beginning, but only that. Physiognomy thus becomes the starting point which can and should lead to the further and deeper investigations of floristic composition, environmental influences and historical development.

Rübel (1930), Du Rietz (1931) and Küchler (1947a, 1949), among others, have proposed methods to classify the vegetation of the world on a physiognomic basis. Each differs fundamentally from the other. Rübel arranged the vegetation of the world into a fixed number of groups and the vegetation of any region was assumed to fit into one of these. Unhappily, Rübel's categories are based in part on physiognomy and in part on ecological aspects. To this inconsistency comes an unfortunate choice in some of his terms. For instance, his *laurisilvae* include not only laurel forests of the Mediterranean region but also the hemlock forests in western Washington, and tropical forests, partly evergreen, partly deciduous, with an admixture of palms, as was shown by Gossweiler (1939) whose interesting map of Angola is based on Rübel's method. This reduced the value of the system to the degree that the meaning of its terms are obscure.

Du Rietz (1931), on the other hand, classifies the life forms of which the vegetation is composed. His method is very detailed and complete but there is no indication that he was at all concerned with mapping. No map based on Du Rietz' classification has come to the attention of the author. Küchler's method also uses life forms. His units lack the fine detail that grace the work of Du Rietz; for instance, there is no way to show fungi because, it is claimed, their part in the physiognomy is negligible. But he had mapping in mind as the main objective in developing his system. Using Köppen's (1931) classification of climates as a model, Küchler uses letters as symbols. By combining different letters as the need arises, he breaks away from Rübel's rigidity. A few maps based on this method have been published to illustrate its range of applicability (Küchler 1948, 1950).

The practical aspects of the physiognomic method are reflected in its use by foresters. The forestry maps (*e.g.*, the map of Lac Letondal) of the Canadian Forestry Services (1948) are based on a physiognomic system very much like Küchler's. The number of units is, however, greatly reduced here and the system is limited to use in the Canadian forests.

Jensen (1947) of the United States Forest Service proposed a more detailed modified physiognomic classification for California and is conscious of mapping problems. He produced four very small maps of the same area, showing life forms, species, density of cover, and vegetation types; the last one is the weakest on account of its terminology. The purpose of Jensen's system is somewhat restrictive, emphasizing the economic exploitation of forests but it should be relatively simple to develop it into one of wide applicability.

The Floristic Approach

Many botanists study vegetation by analysing it taxonomically. The floristic composition becomes the basis of procedure and the units shown on the maps are plant communities characterized by certain species. Of all floristic classifications, the one by Braun-Blanquet (1932) is the best known and the most widely adopted. It is strictly floristic and very carefully thought through to its logical conclusion. It is illustrated by the large

scale map of Montpellier (Braun-Blanquet 1947). The vegetation is divided hierarchically but only the lowest categories are useful on vegetation maps as the higher ones omit important details. Hueck, too, is a follower of the floristic school but greatly simplifies his methods by referring to the species directly and without any reference to a particular hierarchy. In spite of greater detail, his maps are simpler and easier to read and of all strictly floristic maps, his are perhaps the most useful. His method also permits an easy extension into other aspects. While his map of the Riesengebirge (Hueck 1939) is strictly floristic, his map of Germany (Hueck 1938) resembles that of Kuznetzov *et al.* (1928) of the European part of the Soviet Union in that edaphic features have been added. On his floristic map of Niedersachsen (Hueck 1948) he successfully demonstrates the historical development of the vegetation which makes this map one of the greatest modern contributions to the field of vegetation mapping. Another extension of the floristic method is employed by Gaussen (1945b) whose beautiful map of France includes data on the more or less permanent agricultural features such as orchards, pastures, vineyards, and some environmental aspects as well.

In the United States the Forest Service has been publishing several very interesting floristic vegetation maps. Some of the finest examples are the Forest Type maps of Washington and Oregon (Pacific Northwest Forest Experiment Station 1936) which illustrate well the restrictive effect of a limited purpose. As their title implies, they have apparently been designed to satisfy primarily people interested in forest exploitation. The details of the classification vary therefore in direct ratio to the economic usefulness of the species. Of special interest are the large scale maps of California by Wieslander of the United States Forest Service. These excellent and very detailed maps use floristic groups based on considerations of fire hazard. This emphasis of the pyric aspect is rather a novel approach and of the greatest practical significance, especially in California; but the restrictive quality of the purpose is again evident.

The great advantage of the floristic classification is that the vegetation maps show simple facts without resorting to causal relationships. Thus, if *Fagus sylvatica* is shown, there is no ambiguity. A major limitation rests on the fact that the number of important species in a given area may be so large as to make it impossible for the mapper to convey an adequate idea of the vegetation. This is especially true of many tropical and subtropical regions where even very large map scales cannot overcome this difficulty. Indeed, on a map, only a few species of an association can be shown for each place. Hueck (1939) who accurately mapped a relatively very simple vegetation and on the large scale of 1 : 25,000 nevertheless shows as many as 55 different categories of vegetation! One can easily visualize the problems one would encounter in mountainous equatorial regions. In many areas with a more complex vegetation the floristic method of mapping is therefore doomed to break down.

A further disadvantage of the floristic approach to mapping is the general lack of familiarity with the taxonomy of most regions. Even well trained systematists rarely know the species of more than a few limited areas and the great majority of the users of vegetation maps have little or no taxonomic training. Nevertheless, the floristic method is a clear step beyond physiognomy, although the aims may not necessarily be the same.

The Ecological Approach

In itself, the recording of environmental aspects certainly is not mapping vegetation, but climate, soil, and other features have such a strong effect on the distribution of species and plant commu-

nities that attempts continue to incorporate the character of the environment into the map. It is therefore common to find vegetation maps which directly or by implication show one or more ecological aspects. In this country, the first important attempt was perhaps made by Merriam (1898) whose life zones were climatic regions characterized by certain species. The idea is more readily applicable in mountainous areas and it is quite characteristic that it was much more applied and tested in the western states. In Europe, too, the concept of altitudinal zones is used occasionally, again primarily in mountainous regions, as indicated by the vegetation map of Italy (Fiori 1940) and by Markgraf's (1948) map of Albania. Maps of this sort show floristic affinities rather than vegetation, and indeed, Markgraf uses his map to delimit the borders of the Mediterranean region (a floristic region).

These and earlier remarks indicate that a number of authors have preferred to produce complex vegetation maps, based on several concepts, rather than on one single theme. Indeed, a very large number of maps falls into this category and it is quite impossible here to treat them in detail. Two examples will suffice to illustrate different methods.

Few vegetation maps are as well known in this country as the vegetation map of the United States by Shantz and Zon (1923). This excellent map combines the regional, physiognomic, floristic, and ecological approaches by using each one wherever it seems the most useful. The authors do not, therefore, follow a strict plan and there is no unity of system. The different parts of the map are not comparable but the over-all effect is very descriptive.

The second example of a complex approach is the Carte de la Végétation de la France, Feuille Perpignan by Henri Gaussen (1948). This is quite the most ambitious and most advanced type of vegetation map ever to be submitted in print. Gaussen developed his own method of classification in which he, too, combines the regional, physiognomic, floristic, and ecological approaches, and shows both natural and cultural vegetation. He shows, in fact, the natural vegetation and present land use, and the climatic conditions by which both are controlled: and he indicates the natural vegetation as it expresses geographical regions. In addition to present day conditions one can glean from this map the potentially most advantageous exploitation of the area whether such exploitation is now practiced or still a matter of the future.

The natural vegetation is shown to the extent of floristic dominants and physiognomy (trees, shrubs, and herbaceous forms with nine height classes). Basic colors show zones which are above all climatic zones as characterized by index species. The map then shows the degree of reforestation and the species planted. By appropriate choice of color, size, and shape of signs and letters, the land use is indicated in astonishing detail. In addition, there are eight inset maps which further elaborate and supplement the main map. The bewildering wealth of material on this map gives one at first the impression that it is difficult to find the information one may be seeking, but in contrast to the map of the United States by Shantz and Zon, Gaussen presents his data according to a strictly applied unified system which is so logical and clear that one quickly discovers how simply one can obtain all the knowledge which this map so richly offers. At the same time, the manipulation of colors and symbols is so subtle and so superbly done as to represent one of the very highest achievements in the history of making vegetation maps. To a considerable degree, the perfection and the dramatic effect of Gaussen's may rest on an extraordinary familiarity with the region. Outside Europe, there are but few areas where such detailed knowledge is now available and the map serves as an illustration of the amount of work still to be

done in practically all continents other than Europe.

Conclusions and Summary

It is perhaps astonishing that so many vegetation maps have been published which more or less ignore the classifications that various authorities have proposed. Again and again, one finds the mappers develop a new system which they then apply to their own narrow area and which is usually prepared without thought of the vegetation in other parts of the world. Such procedure frequently results in an obscure terminology and a map which does not easily lend itself to comparative studies. Indeed, it is usually impossible to fit two maps of contiguous areas at their common border.

What are then the particular qualities of classifications that tend to make them more readily acceptable? Simply these: 1. The vegetation must be classified into units that can be expressed in simple and unequivocal terms: there must be no doubt about the meaning of the terms used. Before finally deciding on a term, it is best to test it in the greatest possible number of vegetation types. 2. The units of classification must refer to sufficiently distinctive plant communities so that they can be identified in nature. A map should be based on work in the field and must be verifiable there. 3. The classification should be so systematic that one can readily appreciate vegetation maps even if they show areas with which one is totally unfamiliar. We have seen that there are maps which are not based on any particular system and yet seem to fulfill their purpose. To a certain degree this is an illusion. Such maps are usually of limited value to people not acquainted with the area and the local terminology.

It would seem desirable to use existing classifications rather than inventing new ones; there is now a considerable variety available. Where a definite and restrictive purpose calls for special categories not yet provided for, it would still be preferable to use one of the existing classifications of world-wide applicability and make the necessary modifications, but no more. Only by standardization, as far as this is at all possible in mapping vegetation, can the obtained information be appreciated quickly and widely. The unparalleled progress in vegetation mapping during the last two decades, culminating in Gaussen's unrivaled masterpiece, gives one reason to believe that the development must imply improvement in technique, available data, and every other respect, as the demands become ever more exacting.

The relation between classifying and mapping vegetation is very intimate and each one strongly affects the other. Mapping, however, is a method of portraying nature, and the classification must permit the mapper to approximate the true conditions as closely as possible. As a result, we can nearly, though not quite, reverse the sequence, mentioned above, and say that the vegetation comes first and classifying is secondary. Actually, a vegetation map is the meeting ground of two poles: an author's systematic classification and nature's kaleidoscopic arrangement of plants. The degree to which these poles meet depends on the skill and the insight of the mapper, and this, in turn, gives our vegetation maps a distinctly human quality.

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LABORATORY STUDIES ON THE MOISTURE RELATIONS OF LIMONIUS (COLEOPTERA: ELATERIDAE)

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Introduction

These investigations were conducted at Walla Walla, Washington, over a period of 10 years beginning in 1931, as a phase of the ecological studies directed toward the control of the Pacific Coast wireworm, *Limonius canus* Lec., and the sugar-beet wireworm, *L. californicus* (Mann.). Field studies conducted in 1931 on the relation of moisture to the abundance and distribution of *Limonius* spp. in the Walla Walla Valley clearly indicated that moisture was the main limiting factor in the ecology of irrigated-land wireworms. By flooding or drying of the soil, wireworm infestations were effectively reduced. Very effective wireworm control may be obtained by flooding when soil temperatures are above 70 degrees Fahrenheit. Soil dried out by an alfalfa or wheat crop when not irrigated in the summer also effectively reduced wireworm infestations about 74 per cent. Since the matter of encountering and surviving exposure in desiccated soils in the summer is of the first importance to wireworms, it was thought desirable to study the effects of different relative humidities on the various developmental stages of *Limonius canus* and *L. californicus*.

Review of Literature

Few studies on the vital limits of moisture for wireworms in the United States have been reported. Investigations by Langenbuch (1932) and Subklew (1934) on the vital limits of relative air humidities for species of *Agriotes* in Germany showed that the relative humidity of the air in the soil is of utmost importance in maintaining the vitality of all developmental stages, particularly of the larvae. Langenbuch (1932) stated that older larvae are unable to survive in a relatively dry environment notwithstanding their sclerotic tegument. Subklew demonstrated in the laboratory that the development of eggs and larvae of *Agriotes lineatus* L. was normal only in saturated air, and that the resistance of older larvae to decreasing humidity was much greater than that of the younger stages, just as adults were more resistent than pupae. Hawkins (1936) in Maine found that eggs and first-instar larvae of *Agriotes mancus* (Say) died within 1 hour and 18 hours, respectively, upon exposure to the atmospheric humidity (30 to 50 per cent in a room). Campbell (1937) studied the preferences of *Limonius californicus* (Mann.) to temperature and moisture in laboratory tests and noted that wireworms avoided dry soil and died when kept in dry soil. Lane and Jones (1936) and also Campbell and Stone (1938) showed that the prolonged flooding of infested soils with irrigation water while temperatures were high could be used to advantage in reducing wireworm populations. Later Lane (1941) and Shirck (1945) pointed out the beneficial effects of agronomic practices involving soil drying as a means of control.

Methods

Adults and immature stages of the wireworms were exposed to constant temperatures at different humidities.

The eggs and newly hatched larvae were obtained from field-collected adults that deposited their eggs in the laboratory. The older larvae were collected

[1] All work reported in this paper was carried on under the direction of M. C. Lane, to whom the author is indebted for helpful suggestions and criticism.

from baits put out in the field in the spring. Prepupae, pupae, and adults were reared from the field-collected larvae in outdoor soil cages. The larvae and adults were held over winter in the laboratory in moist soil at 10° C. After removal from winter storage an abundance of food was always available, except during the period of desiccation, when the larvae were starved in order to avoid disturbaces because of moisture contained in the food.

The wireworms were desiccated by placing them in a glass desiccator jar with a ground lid, and holding the jar at a constant temperature and humidity. Relative humidities ranging from 10 to 100 per cent were obtained by using solutions of potassium hydroxide or sulfuric acid, as described by Wilson (1921, p. 329) and by Buxton and Mellanby (1934). The humidity in the desiccators was checked by means of a dew-point method. Temperatures were held within a range of 0.5° C.

The insects were held in wire-screen trays or in 1-ounce metal salve boxes placed above the solutions in the desiccators so that the insects might be as much as possible in the desired zone of humidity. Control insects were held in a saturated atmosphere over water or in moist soil. The temperatures were controlled near 20°, 25°, and 30° C.

Daily observations and weighings were made on the desiccating insects. After the insects had become sufficiently desiccated, they were weighed and returned to salve boxes containing moist soil at 20° C. An individual was considered to have recovered when it had regained its original weight, when it crawled actively, or when it had transformed normally to the next stage. All weighings were made on a "Chainomatic" balance sensitive to 0.1 mg. Readings on the water content of normal and desiccated insects were made to determine how great a loss of water was fatal. Body-water content was determined by drying the insects out in glass weighing bottles in an oven overnight at temperatures of 80° to 100° C.

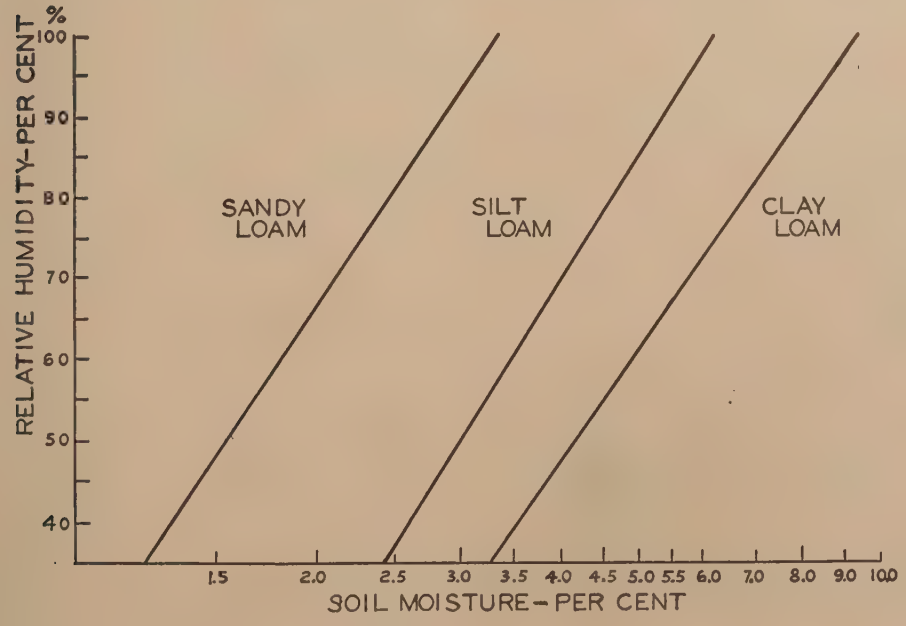

FIG. 1. Relative humidity — soil moisture equilibria at 20° C.

TABLE I. *Water content of* Limonius canus *and* L. californicus

Stage	*L. canus*			*L. californicus*		
	Number observed	Average weight (mg.)	Water* (per cent)	Number observed	Average weight (mg.)	Water* (per cent)
Egg	1,000	0.10	57	3,000	0.07	65
Larva	306	13.9	58	220	18.8	59
Prepupa	20	33.1	60	15	54.8	60
Pupa	9	30.4	63	47	39.8	63
Adult:						
Male	102	20.1	56	47	22.1	55
Female	72	29.4	48	36	35.1	49

* Weighted averages.

In the experiments on the equilibrium between relative humidity and soil moisture, over-dry soils of Yakima sandy loam, Yakima clay loam, and Walla Walla silt loam were exposed to atmospheres of known humidities in the desiccator until equilibrium was reached. In relative humidities of 40 to 100 per cent the soil moisture of sandy loam ranged from 1.3 to 3.3 per cent (fig. 1) and that in silt and clay loam ranged from 2.6 to 6.1 and 3.5 to 9.3 per cent, respectively.

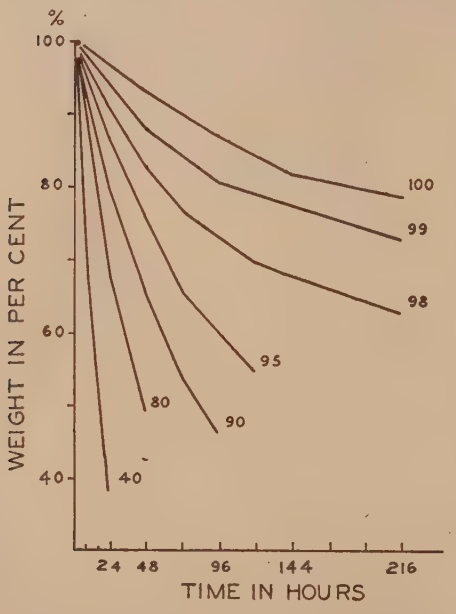

FIG. 2. Rate of weight loss of *Limonius canus* larvae at different relative humidities at 20° C. Numbers indicate relative humidities and curves represent weight as per cent of original weight of an average of 10 larvae for each series.

To obtain information on the moisture preference of larvae a series of glass-tube sections 6 inches long and 1½ inches in diameter were filled with silt loam of known moisture content, and the sections were joined to form a long tube of soil through which the wireworms were permitted to move. The two ends of the tube were corked and the tube was held in vertical position. A moisture gradient was made up in the range of soil moistures from 4 per cent, or air dry, to 15 per cent, or about one half of field capacity. The wireworms, *Limonius canus* Lec., were introduced into the tube at either end or at the center, or were evenly distributed in the sections, as was desired. The experiment was run 4 days in a dark room at constant temperatures. At the close of the experiment the distribution of larvae was determined from the number in each section of the tube.

WATER CONTENT OF THE WIREWORMS

The water content of *Limonius canus* and *L. californicus,* as shown in Table I, ranged from 57 to 63 per cent in the immature stages and from 48 to 60 per cent in the adults. It is evident that there is a decrease in water content on transformation to the adult stage, and that the female contains less moisture than the male.

Vital Limits of Water Loss

Ability to survive desiccation was determined in individually weighed larvae of each species, which were dried at a low humidity until they became inactive, and then weighed again and placed on wet blotters to permit them to recover. The inactive living larvae resume normal activity in about 24 hours. Of 30 *Limonius canus larvae* treated in this manner, 15 survivors had lost an average of 33.8 per cent of original weight, whereas 15 that died had lost 44.8 per cent of original weight. The fatal loss of weight was therefore between 44.8 and 33.8, or about 39.3 per cent. Since only 58 per cent (table I) of the body weight is water, this constitutes a loss of about 68 per cent of water. Twenty-six *L. californicus* larvae were treated as above, with the following results: 16 survivors had lost an average of 33.2 per cent of original weight, whereas 10 that died had lost 46.6 per cent. The fatal loss of weight was therefore about 39.9 per cent. Since in this species only 59 per cent (table I) of the body weight is water, this constitutes a loss of about 67 per cent of water.

Weight Loss in Large *Limonius canus* Larvae

The weight losses of large *Limonius canus* larvae are given in figure 2. The rate of weight loss of large larvae is inversely proportional to the relative humidity. The curves in figure 2 are similar in form, showing a more rapid weight loss at the beginning of the desiccation period followed by a progressive decrease in rate of weight loss. At 99 and 100 per cent relative humidity weight is lost very slowly. At 100 per cent humidity in soil the larvae maintained their initial water content, but when the larvae were held over water at approximately 100 per cent humidity the loss in weight was slow and gradual. Table II shows the percentages of original weight of groups of *Limonius canus* larvae exposed to different relative humidities.

Approximately all the weight loss in the wireworms is due to the evaporation of water. On this basis the amount of water in partially dehydrated larvae was calculated. The partially dehydrated larvae were then completely desiccated, and the observed water content was compared with the calculated water content for the same individuals. The average deviation was not significant; hence a wireworm is not able to conserve body water. The percentage of body water decreases until the insect dies.

Effect of Humidity on Mortality

Adults

At 20° C. and 40 per cent relative humidity both sexes of *Limonius canus* died in 3 days (table III); at 20° C. and 80 to 98 per cent humidity the males died in 6 to 9 days and the females in 10 to 12 days; at 99 to 100 per cent humidity and

Table II. *Percentages of original weight (average 18.5 mg.) of groups of* Limonius canus *larvae exposed for different periods at a constant temperature of 20°C. and different relative humidities. Numbers in parentheses represent dead larvae.*

Exposure (hours)	Relative humidity						
	100%	99%	98%	95%	90%	80%	40%
8	—	—	—	—	—	—	72
24	—	94	91	87	80	69	38 (10)
48	93	88	83	76	66	49 (8)	—
72	—	—	77	66	54	—	—
96	87	81	—	—	46 (9)	—	—
120	—	—	70	55 (9)	—	—	—
144	82	78	68	—	—	—	—
216	79 (3)	73 (2)	63 (6)	—	—	—	—

TABLE III. *Effect of humidity on the mortality of* Limonius canus *adults*

Relative humidity (per cent)	Number of adults		Days required to kill			
			50 per cent		95 per cent	
	Males	Females	Males	Females	Males	Females
Temperature 20°C.						
40	5	5	2	2	3	3
80	5	5	4	5	6	10
90	40	30	5	6	7	10
95	35	30	5	5	9	10
98	35	30	6	8	9	12
99	10	4	15	15	18	16
100	10	5	15	—	25	—
Temperature 25°C.						
98	10	4	3	3	6	6
99	10	5	5	5	12	15
100	10	2	10	—	13	—
Temperature 30°C.						
98	10	4	3	5	5	8
99	10	5	5	5	7	13
100	10	4	7	7	12	12

20° to 30° C. the adults lived 2 or 3 weeks without food.

The females of *Limonius canus* and *L. californicus* were exposed out of soil to atmospheric humidities from 90 to 100 per cent at 20° to 30° C. At 100 per cent humidity they laid their normal number of eggs (about 100 and 200 per female, respectively) and at 99 per cent humidity they laid one-half the normal number. They were unable to lay eggs at humidities of 98 per cent and below. Such reaction to moisture conditions definitely protects the species, and under natural conditions the stimulus to lay eggs undoubtedly depends on the humidity of the soil. Not only is the humidity a factor influencing adult oviposition, but it also affects the survival of eggs, as shown in the next section.

Eggs

Soon after being laid the eggs of both species were exposed out of soil during the 17-day incubation period to humidities of 40 to 100 per cent and a temperature of 20° C. As shown in table IV, the mortality of eggs decreased as the humidity increased. Less than 50 per cent of the eggs held throughout the incubation period succumbed at a humidity above 95 per cent. The mortality was lowest at 100 per cent humidity. In resistance to desiccation *Limonius californicus* eggs were about equal to those of *L. canus*.

TABLE IV. *Mortality of* Limonius canus *and* L. californicus *eggs held for 17 days at 20°C. and at different relative humidities*

Relative humidity (per cent)	*L. canus*		*L. californicus*	
	Number observed	Per cent mortality	Number observed	Per cent mortality
40	50	100	40	100
80	100	92	90	90
90	650	87	1,115	75
95	670	37	1,095	50
98	670	10	1,095	35
99	170	10	95	26
100	670	3	1,115	4

TABLE V. *Effect of humidity on the mortality of first-instar larvae of* Limonius canus *held at 20°C.*

Relative humidity (per cent)	Number observed	Hours required for mortality of	
		50 per cent	95 per cent
40	50	1	6
80	55	3	24
90	126	10	48
95	144	24	72
98	141	48	120
99	100	72	168
100	122	—	—

Failure of eggs to hatch due to deficiency in soil humidity occurs at different moisture contents, depending on the soil type. The eggs of both species of *Limonius* failed to hatch, and in 1 week at 20° to 30° C. they desiccated in sandy loam containing 3 to 5 per cent of water, in silt loam containing 5 to 6 per cent, and in clay loam containing 7 to 8 per cent.

Newly hatched larvae

Desiccation of newly hatched larvae of *Limonius canus* and *L. californicus* was very rapid at atmospheric humidity of 40 per cent and 20° C. (table V). None survived a 24-hour exposure, and at 90 to 99 per cent relative humidity all died in 2 to 7 days. In a saturated atmosphere no newly hatched larvae died in 14 days. Of the various stages studied, these larvae were the easiest to kill, and the eggs were the hardest to kill, by desiccation.

Newly hatched larvae died in 6 days in silt loam containing less than 6 per cent of moisture, at temperatures ranging from 20° to 30° C., with wheat and corn kernels and potato seed pieces as foods. About 10 per cent of the larvae survived 1 month at soil moistures of 6 to 10 per cent. At moistures of 12 to 16 per cent survival for 1 month on the same foods ranged from 15 to 85 per cent.

Older larvae

Larvae of *Limonius canus* and *L. californicus* ranging in size from medium to large, and probably in age from 6 months to 4 years, were exposed to atmospheric humidities from 40 to 100 per cent at 20° C. The time required to kill 95 per cent of the larvae of both species increased from 16 and 24 hours at 40 per cent humidity to 7 and 16 days at 95 per cent humidity (table VI). At 98 to 100 per cent humidity the larvae died in 16 to 35 days. In a saturated atmosphere death resulted from starvation, and not from desiccation. The larvae of *L. californicus* were more resistant to desiccation than were those of *L. canus*. At humidities below 98 per cent *L. californicus* survived about twice as long as *L. canus*.

Death of larvae resulting from deficiency in humidity occurs at different moisture contents, depending on the soil type. In sandy loam containing 3 per

TABLE VI. *Time required to kill large larvae of* Limonius canus *and* L. californicus *at 20°C. and different relative humidities*

Relative humidity (per cent)	Number of larvae observed		Hours required for mortality of			
			50 per cent		95 per cent	
	L. canus	*L. californicus*	*L. canus*	*L. californicus*	*L. canus*	*L. californicus*
40	103	22	6	12	16	24
80	42	22	24	48	48	96
90	87	117	60	144	96	240
95	71	90	69	240	168	384
98	66	84	144	—	384	—
99	32	22	230	—	—	—
100	136	110	480	480	700	840

cent of water and in silt loam containing 5 per cent of water the larvae of both species survived less than 1 week at temperatures of 20° to 30° C. In each case the humidity of the soil air was about 90 per cent. Slightly higher moisture contents were not lethal to larvae.

Soil-moisture Preference of Larvae

To determine the soil-moisture preference of wireworm larvae, three tests were conducted with *Limonius canus*. Five glass-tubes sections were filled with silt loam containing moisture as follows: 4 per cent, 6, 8, 12, and 15 per cent. This range extended from air-dry (4 per cent) to about one-half of field capacity. In the first test 21 larvae were introduced into each section of the tube; in the second test 144 larvae were introduced into the section containing 12 per cent of moisture; and in the third test 215 were introduced into the section containing 15 per cent of moisture. After 4 days most of the larvae in each test were found in the sections having 12 and 15 per cent of moisture. In these sections the humidity of the soil air was about 100 per cent, which appears to be near the optimum range. The larvae avoided the drier soil layers containing 4, 6, and 8 per cent of moisture, where the relative humidity of the soil air was less than 100 per cent.

Effect of Humidity on Metamorphosis

Both species of wireworms are easily killed by desiccation during the transformation from larva to pupa. Thirty-four *Limonius canus* prepupae died after exposure for 2 days at 90 and 95 per cent humidity at 20° C. Eighty-eight prepupae transformed to pupae normally in 1 to 2 weeks at 98 to 100 per cent humidity. The prepupa is like the newly hatched larva in its low resistance to desiccation.

High humidity is necessary for the metamorphosis of the wireworm. At 90 per cent humidity and 20° C. all pupae died in 4 days. At a humidity above 95 per cent at this temperature less than one-half of the pupae died, and the remainder transformed to adults in 3 weeks at 20° C.

At 30° C. all pupae died at 40 per cent humidity in 2 days, and the mortality decreased with an increase in humidity from 40 to 80 per cent. Eight pupae in the late stages of development transformed in 6 days at 90 to 100 per cent humidity. Owing to the shortening of the developmental period at 30° C., pupae survived much lower humidities than at 20° C.

In sandy loam of 3.5 per cent moisture content and a saturated atmosphere held at 20° C., 13 of 14 *Limonius canus* pupae transformed to adults in 22 days. At the same temperature with 3 per cent moisture content and 93 per cent soil humidity, the pupae lived 5 days and none transformed to the adult stage.

These results show that mortality of the eggs, lavae, prepupae, pupae, and adults of *Limonius canus* and *L. californicus* varies inversely with the humidity except at the higher values, where metamorphosis occurs or the individuals die of starvation. The ability of both species to metamorphose is limited to high humidities. A high humidity is also necessary for embryonic development and hatching, as well as for oviposition.

Humidity in the Normal Environment of Wireworms

These studies on the relations of *Limonius* to the humidity of the soil air are in accord with investigations on *Agricotes lineatus* L., published by Langenbuch (1932) and Subklew (1934, pp. 193–194), and have shown conclusively that a saturated amosphere is necessary for their survival. In contrast to the yellow mealworm (Mellanby 1932), larvae of *Limonius* spp. are unable to conserve body water, and when desiccated all the weight loss is due to loss of water. This observation on Limonius is similar to that on the Japanese beetle larva (Ludwig 1936); Ludwig and Landsman

1937) and may be correlated with the fact that normally the larvae of these soil insects are never exposed to the drying effects of the atmosphere.

The inability of wireworms to withstand desiccation as herein demonstrated has been shown by Subklew (1934, p. 222) to be due to the exceptional permeability of the cuticle. The rapid passage of watersoluble arsenicals through the integument, as described by Woodworth (1938), points to the same conclusion. The recent data of Evans (1943) show the osmotic pressure of the haemolymph of *Agriotes* to be approximately equivalent to that of a 0.3 *M* sucrose solution. As the vapor-pressure depression of such a solution is 0.6 per cent and the relative humidity about 99.4 per cent, wireworms exposed to lower humidities will lose water by evaporation. Therefore, the rate of water loss through the integument will be high in comparison with that in insects with less permeable cuticle. The present writer found that *Limonius canus* larvae lost water in a 0.4 *M* sucrose solution.

In the normal environment the soil atmosphere is not always uniformly saturated. The risk of desiccation is therefore real, since the maintenance of the normal water balance is possible only in a saturated atmosphere. Actually, substances in solution reduce the relative humidity slightly. Of greater importance, however, is the hygroscopic property of soils. Thus, for the wireworm, a critical state will be reached when the soil moisture shows a vapor-pressure depression of 0.6 per cent, a value equivalent to (1) a suction pressure of the pF (pico-Farad) scale of 3.9, (2) an osmotic pressure of about 8 atmospheres, and (3) a soil-moisture value of approximately the permanent wilting point of plants. Such conditions are likely to occur when the surface layers of the soil dry out during the summer.

The absorption isotherms of the various types of solids given by Puri, Crowther, and Keen (1925) are instructive from several point of view. These curves show the typical S-shape displayed by many hygroscopic materials, they indicate that if a soil is dried larger amounts of water have to be removed to shift the equilibrium humidity, for instance from 99 to 90 per cent, whereas with further water loss small differences in moisture content cause a rapid drop in humidity. It follows that the saturation deficiencies which may be expected to occur most frequently—for example, during periods when the soil is moderately dry—will be small and therefore difficult to detect experimentally. The values given by Puri *et al.* leave little doubt, however, that such deficiencies must often occur, although their incidence will clearly be affected by climatic conditions and the soil type. Lebedeff (1928), using a specially designed hair hygrograph, was able to demonstrate in the field that high ground temperatures were usually accompanied by measurable saturation deficiencies, although this was only in the surface 10 cm. of soil. Field studies of soil moisture, with a forest duff hygrometer, have been made in the present investigations on the reactions of wireworms to moisture. It has been found that in the summer unirrigated soils with crops of wheat or alfalfa have dried out to 90 per cent humidity at the 6-inch depth.

The reactions of wireworms to humidity as reported by Lees (1943) are evidently correlated with these environmental conditions. He states: "The 'preferendum' is 100% r. h., for in the presence of saturated air all other humidities are avoided; but it is also significant that humidities close to saturation, such as are expected to prevail in the soil, represent just the range over which the reactions are most sensitive; indeed, the whole mechanism of the response is only capable of functioning successfully in the presence of a high humidity."

There is little doubt that humidity is a limiting environmental factor. The present investigation and numerous references

in literature to a migration of wireworms out of the surface layers of the soil during periods of drought (Jones and Shirck 1942, p. 142) are suggestive of the part humidity plays in wireworm behavior. The fact that a saturated atmosphere is necessary for survival of *Limonius canus* and *L. californicus* undoubtedly limits their distribution. These wireworms will not be able to survive in unirrigated soils of the arid and semiarid regions, where saturation deficiences in the soil atmosphere may be expected to occur most frequently.

Summary and Conclusions

An investigation of the humidity relations of wireworms included: (1) determinations of the water content of all stages of *Limonius canus* Lec. and *L. californicus* (Mann.); (2) determination of the rate of water loss in larvae at different relative humidities, as well as the vital limits of water loss; (3) experiments on the relation of humidity to the mortality of *L. canus* and *L. californicus;* and (4) a study of relative-humidity and soil-moisture equilibria in relation to the water balance of the wireworm in its normal soil environment.

The results of each aspect of the problem have been presented and the following conclusions drawn:

1. The water content of *Limonius canus* and *L. californicus* ranges from 48 to 65 per cent of the total body weight.

2. The loss in weight and in water content of *Limonius* spp. is inversely proportional to the relative humidity of the environment.

3. Loss in weight is due to water loss.

4. Adults and eggs are the forms most resistant to desiccation, with pupae and old larvae next in order. Prepupae and newly hatched larvae are the least resistant.

5. The two species of *Limonius* differ only slightly in their resistance to desiccation, and the larvae of both succumb when they have lost about two-thirds of their original water content. A loss of 40 per cent of their original weight is fatal.

6. The fact that a saturated atmosphere is necessary for survival undoubtedly limits distribution of these wireworms to irrigated soils of semiarid regions.

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A STUDY OF TWO FOREST STANDS IN MINNESOTA WITH AN INTERPRETATION OF THE PRAIRIE–FOREST MARGIN [1]

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INTRODUCTION

The deciduous forest extends northwestward in the northern half of Minnesota as a narrowing band between the coniferous forests on the east and the prairies on the west. This is well illustrated by Upham's original map of the vegetation of Minnesota and the various reproductions of it (Upham 1884, Rosendahl and Butters 1928, Daubenmire 1936, Buell and Wilbur 1948). As is characteristic of such major vegetational transitions, the contacts of the deciduous belt with adjacent formations are usually not sharp. There is evidence that they are not at present in a state of equilibrium. As Griggs (1946) infers, such contacts probably seldom are.

East of the hardwood belt there is a broad transition zone between it and the coniferous forests where, in the pattern of distribution of the vegetation, the conifers form the continuous phase and the maple-basswood community the discontinuous phase. Continuing eastward in northern Minnesota there are increasingly greater distances between the stands of the hardwood forest. West of the hardwood belt the continuous phase gradually shifts from deciduous forest to prairie. Isolated stands of trees or clumps of shrubs occur along the easternmost margin of the prairie. The transition to prairie is sharper than that to coniferous forest, in some places being rather abrupt.

In the deciduous-conifer forest tension zone several studies have been concerned with the relative status of the forest communities. Bergman and Stallard (1916) and Bergman (1923) came to the conclusion that the *Pinus strobus-Pinus resinosa* communities represent the climatic climax in the northern part of the state. Several workers who have subsequently centered their efforts in the Itasca Park area stated either directly or by inference that they did not agree with these authors. Lee (1924), for instance, came to the conclusion that the maple-basswood forest represents the climax in Itasca Park. Kell (1938) states that the pattern in this transition zone cannot be so simply resolved. She supports the polyclimax view, stating that there are three climaxes in Itasca Park, the maple-basswood on fine mineral soils, the fir-spruce-birch climax on coarser textured mineral soils, and the ash-elm-fir on peat.

It is certain that on mineral soils there are two communities that have climax characteristics, the maple-basswood and the fir-spruce-birch. Kell's results would suggest that the distribution of the two depends on the soil pattern, minor variations in soil texture favoring the one over the other. The fir-spruce-birch seems to be slightly more favored by a very recent climatic swing, although it has been unable to displace the hardwoods (Buell and Gordon 1945). Where the two climaxes are contiguous, ele-

[1] This paper is a contribution from the University of Minnesota Biological Station, Itasca Park (paper no. 10) and from the Botany Department of Rutgers, the State University of New Jersey.

ments of the fir-spruce-birch climax are able to migrate into the hardwood community at points, although their establishment is not successful. On the other hand, maple-basswood ground cover and reproduction are absolutely prevented from entering the conifer community, a prohibition that Buell and Gordon (1945) believed to be correlated with light intensity.

Farther east, in Itasca County, Grant (1934) found a fir-basswood climax community. The author states that this climax forest is of a transitional nature and believes that it is probably the climax community over most of the coniferous regions of Minnesota except the extreme northeastern corner.

As mentioned above, on the west, at the latitude of Itasca Park, the transition to the open prairie is usually through what has been called the "brush prairie" (Ewing 1924). Passing westward from the hardwood forest, at first the brush consists primarily of scrubby growth of *Quercus macrocarpa* [2] with *Corylus americana* and *Rhus glabra.*

It forms the continuous phase with isolated stands of the Acer-Tilia community established in some localities. Continuing farther westward the prairie soon becomes the continuous phase and the brush the discontinuous phase. *Quercus macrocarpa* is continually less important and *Populus tremuloides, P. balsamifera, Prunus serotina* and various shrubs become increasingly predominant in the clumps. The brush decreases uniformly as the flatness of the country becomes more marked.

The whole picture of the vegetational boundary is in part tied up with topography or related edaphic conditions, the present western limit of the deciduous forest being roughly coincident with the eastern margin of glacial Lake Agassiz and the western limit of the Bigstone morainic system. However, it is not yet understood why the forest-prairie ecotone at the latitude of this study lies at present along the eastern margin of glacial Lake Agassiz. The level expanses of the glacial lake bottom end in a series of beach ridges behind which is increasingly uneven territory until the rolling morainic country is reached. The first appearance of maple-basswood forest occurs on the high moraines east of Lake Agassiz. More or less well developed moraines interspersed with outwash plains continue from there eastward all the way across the state. The moraines in the western portion of the state are composed of "gray drift" which had its origin in the limestone areas to the northwest. As a result, the parent materials from which the soils of the region have been derived are largely calcareous.

The present study was begun with the idea of comparing a maple-basswood stand at the prairie margin with one located well within the deciduous-conifer forest tension zone to the east. It was hoped that a study of the contrasts in structure, composition, vitality and history of the two stands together with the differences in the climatic, edaphic, and biotic environments might give valuable information concerning the dynamics of prairie-forest and deciduous-conifer tension zones.

The two hardwood communities upon which the present study is based are both located on moraines. One is in the hardwood-conifer forest tension zone. The other is one of the westernmost stands of the maple-basswood community at the same latitude. The former is in Itasca Park along the Bohall Trail west of Lake Itasca, specifically in the southwest quarter of Section 10, T 143 N, R 36 W in Clearwater County. It is located on rolling upland about 80 feet above the lake and half a mile west of it. It is surrounded by extensive forest predominantly coniferous and aspen. The other stand lies about thirty miles west of this

[2] In northern Minnesota it is only the variety, *Quercus macrocarpa* var. *olivaeformis,* which is present. The nomenclature for this paper follows Rosendahl and Butters (1928) for trees and shrubs, and Fernald (1950) for all others.

on the moraine east of Waubun in Mahnomen County. It is located specifically in the west half of Section 17, T 143 N, R 40 W. It occupies a low hilltop and gentle slopes. The north and east slopes descend to a small stream. On the south and west the forest opens abruptly onto cultivated lands.

The important climatic comparisons between the areas have been previously summarized (Buell and Wilbur 1948).

The authors are indebted to Drs. W. S. Cooper and D. B. Lawrence for their critical reading of the manuscript or parts of it and for their valuable suggestions.

Methods

In sampling the vegetation of the two stands, straight lines were established through the community. Along these lines 10×10 meter quadrats were laid out at intervals of 10 meters. Twenty-five such quadrats were established for each stand. Diameters of all trees 1 inch d.b.h. (diameter breast height) and over on each of the quadrats were determined and recorded by species. Within the 10×10 meter quadrats rectangular plots 2×8 meters were measured off and all tree saplings less than 1 inch d.b.h. and over 1 foot high and all shrub stems arising from the ground were counted. Four $\frac{1}{4} \times 4$ meter plots were established, one in each corner of the large quadrats. In these small quadrats a count was made of the number of herbs and tree and shrub seedlings. For most of the herbaceous species this was a count of the number of above-ground stems, as in Polygonatum, or the number of clumps, as in Carex.

From the data obtained the density and basal area per 2,500 square meters of trees over 1 inch d.b.h. were calculated. Density of tree saplings and shrub stems was determined on 400 square meters, and density of herbs and woody seedlings on a total of 100 square meters.

The term density in this paper is used to express the number of individual plants, stems or clumps, per unit area. Frequency is used to express the occurrence of species in the quadrats and is given in terms of the per cent of the quadrats in which the species was found. This is essentially the usage of Oosting (1948) and Daubenmire (1936).

In constructing life-form spectra, species have been assigned to the life forms on the basis of previous work by Buell and Wilbur (1948).

Light determinations were made with a Weston photometer. In the Waubun stand 200 readings were made in the woods. Three sets of 30 readings of full sunlight were taken in the middle of the highway immediately before, after the first hundred, and at the completion of the forest readings. The procedure for taking the forest readings was to mark out a straight line in the forest with a tape and make readings at about 6 feet from the ground at every meter mark on the tape. A similar procedure was used in obtaining light readings in the Itasca stand. The readings for the two stands were of necessity made on different days but under similar meteorological situations. The figure obtained for the Itasca stand is substantiated by earlier work in the same forest by Buell and Gordon (1945).

The soils were studied by digging pits into or through the B horizon. One face of the pit was scraped clean and measurements and description of the horizons were made. Collection of soil for mechanical analysis was made in the Itasca stand by scraping a composite sample from the leached A horizon. All other samples were taken with a view to determining weight-volume ratio. For this purpose 11 ounce soup cans with a hole punched in the floor were used. The use of this convenient and inexpensive sampler is suggested by Dr. D. B. Lawrence. The cans are 10 centimeters deep and were driven in vertically at various levels as indicated by the data.

Mechanical analyses of the soils were made using the Bouyoucos (1936) hydrometer method. The organic matter

content of the soil was determined by Schollenberger's (1931) method. The pH of soil samples was obtained in the laboratory with the Beckman pH meter. The dry soils were soaked for 24 hours in distilled water before the determination was made. The soil-water ratio used was 1 : 2.5.

Results

1. Description of the Itasca stand

The forest at Itasca consists of three more or less distinct tree layers, a shrub layer, an herb layer, and a very discontinuous moss layer. The uppermost tree layer consists of the scattered high crowns of the pines. The main, continuous canopy of the forest presents an uneven upper surface with the crowns of the less shade-tolerant trees forming irregularities by extending somewhat above the general canopy of the dominant species. Below the latter is another rather complete layer formed by the subcanopy tree, *Ostrya virginiana,* and the transgressives of the dominant species. The shrub layer is very poorly developed. Except under openings in the canopy where a local thicket may develop, the forest is generally open with an occasional shrub, but there is a rather complete herb covering. The moss layer is poorly developed except on rotting logs and stumps which are usually heavily covered.

In the Itasca stand *Acer saccharum*

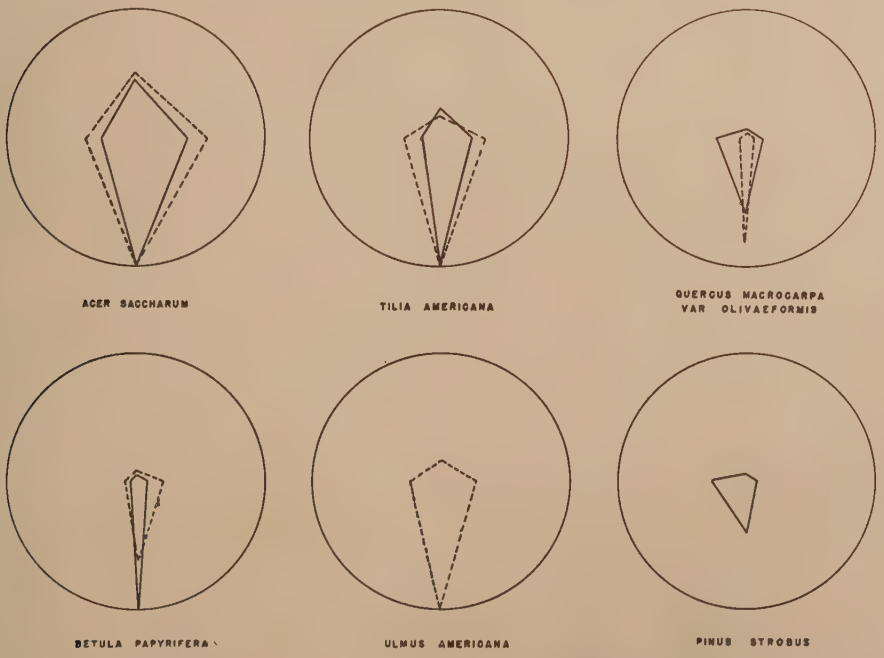

Fig. 1. Phytographs of the important tree species; the Itasca stand in solid line, the Waubun stand in broken line. These are constructed in the same way as those made by Daubenmire (1936) and Eggler (1938) with the vertical radius above the center representing per cent of total density of stems 10 inches d.b.h. and over, the radius to the right of the center representing frequency or per cent of the 25 quadrats (10 × 10 meters) in which stems 10 inches d.b.h. or over occurred, the radius below the center representing the number of size classes as separated in tables II and V by which the species is represented, and the radius to the left of the center representing dominance given as aggregate basal area of stems 10 inches d.b.h. and over in per cent of basal area of all species.

TABLE I. *Dominance of species expressed as square feet basal area at breast height. Based on sampling area of 2,500 square meters. Italics in the last two columns emphasize the greater basal area where a species is present in both stands.*

	1–3.9 inches d.b.h.		4–9.9 inches d.b.h.		10 inches or more d.b.h.		Total basal area in sq. ft. per 2,500 sq. m.		% of total basal area	
	Itasca	Waubun	Itasca	Waubun	Itasca	Waubun	Itasca	Waubun	Itasca	Waubun
Acer saccharum	2.44	2.29	7.66	11.05	12.86	24.37	22.96	37.71	29.3	*41.1*
Tilia americana	0.04	0.48	5.86	3.86	6.49	16.58	12.75	20.92	16.3	*22.8*
Ostrya virginiana	1.55	2.50	1.10	2.66	—	—	2.65	5.16	3.4	*5.6*
Betula papyrifera	0.14	0.13	3.06	1.79	1.66	4.81	4.86	6.73	6.2	*7.3*
Fraxinus pennsylvanica	—	—	0.10	0.31	—	—	0.10	0.31	0.1	*0.3*
Quercus macrocarpa var. *olivaeformis*	—	0.05	—	—	10.82	1.93	10.82	1.98	*13.8*	2.1
Ulmus americana	—	0.05	—	0.38	—	14.56	—	14.99	—	16.4
Populus balsamifera	—	0.02	—	2.64	—	0.57	—	3.23	—	3.5
Ulmus fulva	—	0.03	—	—	—	0.66	—	0.69	—	0.8
Pinus strobus	—	—	—	—	11.73	—	11.73	—	15.0	—
Abies balsamea	0.70	—	2.69	—	—	—	3.39	—	4.3	—
Populus tremuloides	—	—	2.37	—	2.56	—	4.93	—	6.3	—
Acer rubrum	0.35	—	0.83	—	0.68	—	1.86	—	2.4	—
Quercus borealis	0.07	—	1.34	—	—	—	1.41	—	1.8	—
Picea glauca	0.07	—	—	—	0.55	—	0.62	—	0.8	—
Fraxinus nigra	—	—	0.31	—	—	—	0.31	—	0.4	—
Totals	5.36	5.55	25.32	22.69	47.35	63.48	78.39	91.72		

and *Tilia americana* are by far the most important trees. This is well shown by the phytographs (fig. 1) where these two species are represented by the largest polygons. Not only do they have a greater total basal area than any other species, but they are abundant and evenly distributed in the stand as well as effectively reproducing themselves (tables I and II). The exceedingly high number of Acer seedlings is striking. The number of seedlings of Tilia is very much less than that of Acer. Very few of this small number of Tilia seedlings reach sapling size. Only one sapling definitely of seedling origin was found in this stand. Most of the reproduction of this species has its origin as stump sprouts. In addition to these two species *Ostrya virginiana* is likewise abundant, evenly distributed, and successfully reproducing itself. Being potentially only a small tree, however, it does not contribute much to the basal area.

Eleven other arborescent species are found in the community. Three of them, *Pinus strobus, Abies balsamea,* and *Picea glauca* are conifers. *Pinus strobus* is represented by a few large individuals whose crowns begin above the general level of the canopy of the broad leaf trees and tower considerably above it. This species is absent from all size classes between these large individuals and the seedling class.

The other two conifers, *Picea glauca* and *Abies balsamea,* are boreal climax species and together make up the bulk of certain forest communities that are in contact with the Itasca stand as well as being generally extensive throughout the Itasca area. The conifer forest, is, indeed, so nearly continuous that Upham included Itasca Park in the conifer region on his map. An occasional tree of Picea is found among the hardwoods and its seedlings appear to be somewhat more successful in their shade than those of the pine, as one would expect on the basis of studies made by Shirley (1945) in this region. Abies succeeds in establishing itself in temporary small groups or "islands" but neither the spruce nor the fir is a very successful competitor with the climax hardwoods (Buell and Gordon 1945).

The status of associated broadleaf trees in the community varies with the species. *Betula papyrifera,* like Abies and Picea a member of the boreal climax forest, is present and successfully reproducing in the Itasca hardwood forest. The mature trees of this species have most of their crowns above the canopy of the maple and basswood trees. This is also true of *Quercus macrocarpa* which is present as large, old trees with tall, clear trunks holding their foliage above the general forest roof. Like white pine, its reproduction is not successful. The other oak, *Quercus borealis,* is more successful at reproduction, but there are few trees of this species and they have not yet reached large size. *Populus tremuloides* is another species whose crowns project above the forest. The data in table II suggest that this tree is well represented in both the seedling and sapling class. Actually there are no seedlings nor are there saplings of seedling origin. The many small individuals represented in the data are root sprouts which appear unthrifty and seldom attain tree size in the shade of the forest. The other tree species, *Acer rubrum, Fraxinus nigra, F. pennsylvanica,* and *Ulmus americana* are less important in the community. No large elms occurred on any of the quadrats. It is rare as a tree in the community.

Age determinations by increment borings were attempted for a number of broadleaf trees. One of the large trees of *Quercus macrocarpa* showed 308 rings to the rotten center. Borings were made in all other hardwood species except *Acer saccharum* and *Ostrya virginiana.* Heart rot is common and age determinations were not satisfactory. Counts of from 40 to 90 rings outside the rotten centers are suggestive only. The authors believe that the majority of trees other than the pines and bur oaks are from 100 to 150 years of age. The largest trees of the principal species were sought out and measured. Maximum diameters (d.b.h.) in inches were: *Acer saccharum* 14.5, *Tilia americana* 17.7, *Ostrya virginiana* 6.0, *Quercus macrocarpa* 32.0 and *Betula papyrifera* 19.6. Height determinations showed *Acer saccharum* to be around 60

TABLE II. *Density and frequency of trees in the Itasca stand*

	Individuals less than one inch d.b.h.†				Individuals 1 inch d.b.h. and over						Totals
	1 ft. tall or less		More than 1 ft. tall		1–3.9 in.		4–9.9 in.		10 in. and over		
	D	F	D	F	D	F	D	F	D	F	D
Acer saccharum	21,900	100	1,125	76	63	68	39	60	17	40	23,144
Tilia americana	900	60	200	36	6	24	23	52	8	24	1,137
Ostrya virginiana	2,575	84	3,294	92	38	68	8	28	—	—	5,915
Quercus macrocarpa var. *olivaeformis*	275	36	81	36	—	—	—	—	3	12	359
Quercus borealis	575	44	144	40	1	4	4	12	—	—	724
Betula papyrifera	225	16	19	12	2	8	11	24	2	8	259
Abies balsamea	200	24	—	—	26	40	14	32	—	—	240
Picea glauca	75	12	6	4	1	4	—	—	1	4	83
Pinus strobus	600	44	—	—	—	—	—	—	2	8	602
Populus tremuloides	50	8	287	48	—	—	7	16	4	12	348
Acer rubrum	950	64	44	8	6	24	5	12	1	4	1,006
Fraxinus nigra	125	16	6	4	—	—	2	8	—	—	147
F. pennsylvanica	—	—	13	8	—	—	1	4	—	—	14
Ulmus sp.	100	16	6	4	—	—	—	—	—	—	106
Totals	28,750		5,225		143		114		38		34,084

† The number of individuals counted in the quadrats of these categories have been multiplied by the proper figure to compensate for the smaller sized quadrats used.

TABLE III. *Density and frequency of shrubs in both stands. Density figures refer to the number of stems per 400 square meters.*

	Itasca		Waubun	
	D	F	D	F
Corylus rostrata	74	64	95	52
Ribes cynosbati	6	8	59	76
Prunus virginiana	—	—	22	48
Celastrus scandens	—	—	17	8
Acer spicatum	13	20	15	4
Cornus alternifolia	—	—	10	24
C. rugosa	—	—	6	4
Viburnum affine	11	20	5	12
Prunus nigra	2	4	4	8
Lonicera dioica	—	—	2	8
Rubus strigosus	40	20	2	4
Ribes triste	—	—	1	4
Dirca palustris	31	68	1	4
Rosa blanda	—	—	1	4
Amelanchier humilis	2	4	—	—
Cornus candidissima	1	4	—	—
Totals	180		240	

feet and *Tilia americana* as high as 70 feet. *Populus tremuloides, Betula papyrifera* and *Quercus macrocarpa* represent a "super-canopy" group up to 90 feet. The scattered individuals of *Pinus strobus* tower well above these.

The shrub layer is rather sparsely developed for a deciduous forest. The species occurring on the quadrats are listed in table III. There are 9 species and a total of 180 stems per 400 square meters. This is a rather low value for shrub density. The three species contributing most to the shrub density are *Corylus rostrata, Rubus strigosus* and *Dirca palustris.* These three shrubs also contribute most to shrub cover. The plant ecology class from the University of Minnesota Biological Station working in the same stand determined cover of the shrub layer using a modification of Bauer's transect method (Bauer 1943, Buell and Cantlon 1950). These data show that the same three species contribute most of the shrub cover, with *Dirca palustris* contributing 55 per cent, *Corylus rostrata* 40 per cent and *Rubus strigosus* 25 per cent. The total cover of the shrub layer was found to be only 4.6 per cent, indicating very poor development of this layer, a point already suggested by the low density mentioned above.

In contrast, the herb layer is essentially

TABLE IV. *Density and frequency of herbs and light penetration values for each stand. Rank refers to density, those with highest density having the lowest rank. Density here refers to the number of individuals, stems or clumps per 100 square meters. The ten highest ranking species of each stand are included.*

Species	Waubun			Itasca		
	D	F	Rank	D	F	Rank
Uvularia grandiflora	937	100	1	271	96	3
Carex pensylvanica	758	100	2	2,964	100	1
Solidago flexicaulis	462	92	3	19	28	23
Carex pedunculata	138	72	4	262	72	4
Aralia nudicaulis	144	88	5	82	76	14
Thalictrum dioicum	102	92	6	41	76	18
Pyrola rotundifolia	80	28	7	2	4	42
Oryzopsis asperifolia	75	68	8	135	88	9
Aralia racemosa	48	72	9	—	—	—
Phryma leptostachya	45	48	10	—	—	—
Aster macrophyllus	2	8	33	401	100	2
Hepatica americana	—	—	—	254	100	5
Rubus pubescens	3	8	30	171	64	6
Galium triflorum	9	20	23	153	72	7
Luzula campestris	—	—	—	141	60	8
Uvularia sessilifolia	34	56	13	108	84	10
Total of all species	3,301	—	41	6,942	—	45
Light penetration of canopy		2.4%			9.8%	

TABLE V. — *Density and frequency of trees in the Waubun stand*

	Individuals less than 1 inch d.b.h.†				Individuals 1 inch d.b.h. and over						Totals
	1 ft. tall or less		More than 1 ft. tall		1–3.9 in.		4–9.9 in.		10 in. and over		
	D	F	D	F	D	F	D	F	D	F	D
Acer saccharum	1,625	84	919	92	92	72	54	84	30	56	2,720
Tilia americana	125	20	137	40	21	48	13	32	10	36	306
Ostrya virginiana	875	48	637	72	106	88	15	40	—	—	1,633
Quercus macrocarpa var. *olivaeformis*	125	20	31	12	—	—	3	12	2	8	161
Betula papyrifera	—	—	—	—	3	8	8	20	5	20	16
Populus balsamifera	25	4	12	4	1	4	8	12	1	4	47
Fraxinus pennsylvanica††	325	28	6	4	—	—	1	4	—	—	332
*Ulmus americana**	300	28	6	4	4	4	1	4	10	28	330
U. fulva			6	4	2	8	—	—	1	4	
Totals	3,400		1,754		229		103		59		5,545

† Individuals in these two categories were multiplied by the proper figure to compensate for the smaller quadrats used.
†† Including the var. *lanceolata*.
* Seedlings and totals of the two species of Ulmus are not separated in the data.

continuous. The very high population of sedges, *Carex pensylvanica* and *C. pedunculata*, give the forest floor a "grassy" appearance. *Aster macrophyllus* which is almost ubiquitous in Itasca Park has a high density in the maple-basswood community. Two other species, *Uvularia grandiflora* and *Hepatica americana*, are present in large numbers and are distributed through the community. In all there are 45 species of herbs represented in the quadrat data. The total number of plants, shoots or clumps counted on the 100 square meters sampled is 6,942 (table IV).

Light readings at 6 feet indicate an average light penetration of the canopy of about 9.8 per cent. This figure compares well with that obtained earlier in the same community by Buell and Gordon (1945).

The soil is a well developed podzol. The organic horizon is made up of 2 cm. of litter under which is mor humus (Lutz and Chandler 1946: 171) 5 centimeters thick. There is a sharp transition from this to the mineral A horizon. The latter averages about 16 centimeters thick. This is underlain by a reddish-brown B horizon.

The mechanical analysis of the A horizon, based on 5 samples, varies from 35.5 per cent to 69.6 per cent sand, 19.9 to 49.4 per cent silt, and 10.5 to 17.1 per cent clay. Practically all of the clay is fine clay (0.002 mm. and finer). The pH of the A horizon ranges from 4.4 to 4.6. Soil from the A horizon is readily broken down into fine powder when dry and chunks of this soil slake or crumble rapidly when placed in water.

2. Description of the Waubun stand

In the Waubun stand there are but two tree layers, the one consisting of the crowns of the dominants and one immediately below composed of the crowns of Ostrya and the transgressives of the dominant species. The shrub layer is sparse, although somewhat less so than at Itasca, but the herb and moss layers are conspicuously poorer in cover.

In this stand *Acer saccharum* and *Tilia americana* are again the most important trees of the community (fig. 1). These species have the highest total basal area

and both are well represented in all size classes (table V). Most of the individuals indicated as basswood saplings in the table are of sprout origin although several saplings of seedling origin were discovered. *Ostrya virginiana,* an understory tree, is also of primary importance in the stand. In the 1–3.9 inch class it has the highest density, frequency, and basal area (table I). Like the maple and basswood it is a permanent member of the community. In addition to these three species there are six other arborescent species present, none conifers. *Betula papyrifera* is the only species which is a member of the boreal climax forest. No new birch reproduction was observed at the time of sampling and no evidence was discovered to indicate that the species has reproduced successfully in the last few years.

Populus balsamifera is another northern species present but it is typically a member of successional communities in the northern conifer region. It is not very successful in maintaining a place in the hardwood community. The few individuals classified in table III as seedlings and saplings are actually root sprouts which do not thrive in the shade of the forest.

Quercus macrocarpa is represented by a few individuals of sizes comparable to those of the dominant species. No individuals exceed in diameter the largest Acer or Tilia trees. The straight trunks and the lack of large, low branches suggest that they are forest grown trees.

Ulmus americana and to a lesser extent *U. fulva* are conspicuous in some parts of the community particularly lower down on the slopes. *Fraxinus pennsylvanica* is the least important arborescent member of the community.

Increment borings were made in a number of trees but the same problem of rot at the center prevented satisfactory ring counts. A better idea of the age of the stand was obtained at one point where a number of trees had been cut recently and the stumps of three sugar maples in the area were in good enough shape so that ring counts could be made. The trees were 12, 13, and 14 inches in diameter at stump height (approximately 2 feet). They showed 130, 130, and 137 rings, respectively. Since they had been cut in 1941, they must have started growing about 1810.

The heights of several trees were determined. A tree of *Tilia americana* measured 70 feet, of *Acer saccharum* 53 feet, of *Ulmus fulva* 74 feet, and of two trees of *Populus balsamifera* 65 and 70 feet, respectively. The trees chosen were among the largest of each species that were in a position where determination could be made. The average height of the forest canopy of the Waubun stand is 5 to 10 feet lower than the dominant canopy of the Itasca stand.

The largest trees measured (in inches d.b.h.) of several species were: *Acer saccharum* 22.5, *Tilia americana* 26.5, *Ostrya virginiana* 10.7, *Quercus macrocarpa* 22.2, *Betula papyrifera* 17.2, and *Ulmus americana* 23.6.

The shrub species occurring on the quadrats are listed in table III. There are 14 species and a total of 240 stems per 400 square meters. The 3 species contributing most to the shrub layer are *Corylus rostrata* with a density of 95, *Ribes cynosbati* with a density of 59, and *Prunus virginiana* with a density of 22 stems per 400 square meters. As at Itasca the shrub layer consists of rather widely separated plants.

In the herb layer 41 species of plants were represented in the quadrat data. Of these *Uvularia grandiflora, Carex pensylvanica,* and *Solidago flexicaulis* are present in greatest numbers. The total density, *i.e.,* the number of plants, shoots, or clumps per 100 square meters sampled, is 3,301 (table IV).

Light readings at 6 feet indicate an average light penetration of the canopy of 2.4 per cent.

The soil profile as seen superficially along the road cuts looks like a chernozem (fig. 2). Some of the characteristics of

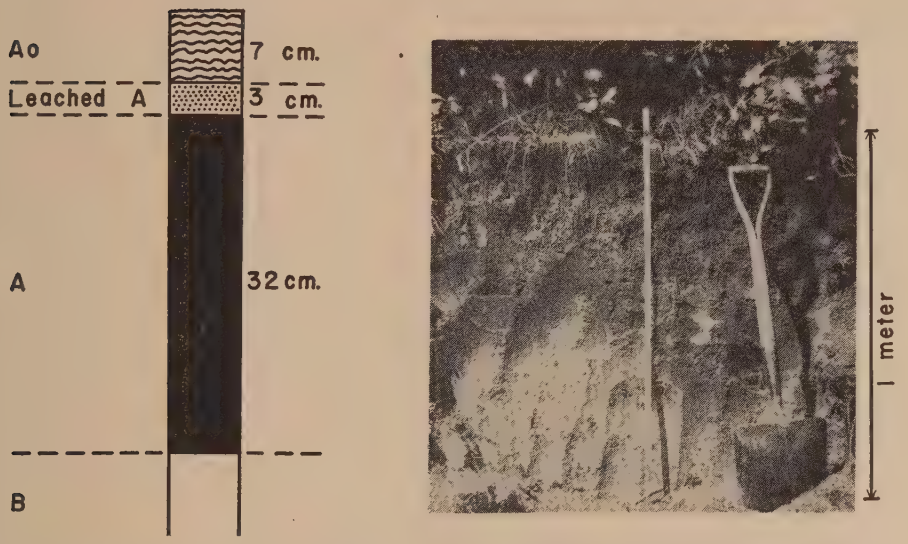

FIG. 2. The soil profile at the Waubun stand. The diagram at the left is constructed from notes made on the soil pits. The figures are averages for the thickness of the horizons shown. The photograph shows the wall of one of the pits. Details of the A horizon cannot be distinguished in the picture.

the profile can be seen in table VI. The litter is about 2 centimeters thick. Below it the mull humus (Ao) averages 7 centimeters. There is no definite line separating this humus layer from the mineral A horizon. The upper 3 centimeters of mineral soil are dark gray in color, contrasting with the lower part of the A horizon especially when dry. The soil of this layer has a laminated or platy structure. Below this leached zone the A horizon is dark gray-black with a very well developed crumb structure. Chunks of soil from the A horizon do not slake in water. The A horizon excluding the leached upper 3 centimeters averages 32 centimeters in thickness. Below it the B horizon averages 33 centimeters or more in thickness. (The soil pits being only 70 centimeters deep did not all extend to the C horizon.) The B horizon is light brownish in color marked with black or occasional reddish-brown streaks which become more distinct below. A prismatic structure is present which also becomes more pronounced in the lower part. The prisms are less than 1 centimeter in diameter and covered with a dark brown to black coating. The C horizon is light gray in color and is structureless. The presence of calcium carbonate is indicated by effervescence with the application of hydrochloric acid. The soil profile fits the description of a characteristic degraded chernozem (Joffe 1949, Joel 1933).

The increasing weight-volume ratio with depth is related to variation in three soil properties: decrease in organic matter, decrease in aggregation, and accumulation of colloids at the lower level (see table VI). The mechanical analysis of the A horizon suggests a rather fine soil. The clay content is from 28.8–34.6 per cent. The clay increases over 12 per cent in the B horizon, a shift that can be expected where podzolization has occurred. The pH of the humus indicates it to be only slightly acid. The 3 centimeter leached layer at the top of the mineral A horizon has a pH of 4.7, the most acid of the profile. The rest of the A and the B horizons have a slightly higher pH, though still acid. The C horizon, or the

parent material, is alkaline with a pH of 7.6. This figure reflects its high calcium carbonate content.

3. Comparison of the two stands

The arborescent layer of the two communities differs in species composition, in total density and total basal area, in height and in relative importance of the species making up the canopy. Not only is the arborescent flora richer at Itasca, 14 species compared with 9, but the total density in the Itasca stand greatly exceeds that at Waubun. Among trees 1 inch d.b.h. and over the Waubun forest has many more individuals particularly in the 1–3.9 inch class and in the 10 inch and over class. The intermediate size class is about the same in both. The Waubun stand is also superior in total basal area. This difference is produced entirely by the largest size class, the other size classes being the same in both stands. Not only is the total basal area greater at Waubun but the basal area of all species common to both stands, except *Quercus macrocarpa,* is greater there. In this connection it is significant to mention that the maximum diameter of each of the dominant species occurs in the Waubun stand. In contrast the Itasca forest is higher, both because of the presence of numerous "super-canopy" trees and because the maple-basswood canopy itself is higher.

The two plant communities are alike in their dominant species, *Acer saccharum* and *Tilia americana,* and in the

TABLE VI. *Certain characteristics of the soil at the Waubun stand. Samples from the C horizon effervesce with HCl. No weight-volume ratio samples contained more than 0.04% of particles over 2 mm. The two values in parentheses directly below those for the per cent clay, and labeled "Prec." and "Susp." are the two fractions representing: Prec. = the amount settling out of the soil suspension in the second hour, and Susp. = the amount still left in suspension at the end of two hours. "pH by horizons," given in the sixth column, refers to a third station, samples for determination being taken from the middle of the horizon, without regard to depth*

Horizons	Depth below Ao horizon	Active weight-volume ratio		Mechanical analysis	pH by depth		pH by horizons	Organic matter	
		Sta. 1	Sta. 2	Sta. 1 Sta. 2	Sta. 1	Sta. 2		Sta. 1	Sta. 2
Ao							6.5		
A	0–10 cm.	1.23	0.94	Sand—35.2—27.6 Silt—36.0—36.8 Clay—28.8—34.6 Prec. (3.2) (6.0) Susp. (25.6) (29.6)	6.5	6.7	(leached A 4.7)	3.64	3.54
	20–30 cm.	1.16	1.16	Sand—35.6—26.4 Silt—30.0—30.0 Clay—34.4—43.6 Prec. (4.8) (6.0) Susp. (29.6) (37.6)	6.5	5.9	(A1 5.8)	3.07	2.42
	30–40 cm.	1.60	1.16				(A2 5.8)		
B	40–50 cm.	1.59	1.24	Sand—21.2—13.2 Silt—32.0—30.0 Clay—46.8—56.8 Prec. (6.0) (12.0) Susp. (40.8) (44.8)	7.7	6.5	(B 5.0)	1.80	1.16
	50–60 cm.	1.64	1.58						
C	60–70 cm.	1.61	1.62	Sand—14.4—55.2 Silt—42.0—22.4 Clay—43.6—22.4 Prec. (8.8) (6.4) Susp. (34.8) (16.0)	7.9	7.4	(C 7.6)	1.00	0.35

position of the very important understory tree, *Ostrya virginiana.* These three species have the highest density and the most vigorous reproductive capacity of all tree species present in either stand. They differ in the two communities in that they grow taller at Itasca but have attained greater maximum diameters at Waubun.

Pinus strobus at Itasca is present as large, old individuals but does not occur in the vicinity of the Waubun stand. One first sees it about three miles east of the stand. Like *Pinus strobus, Quercus macrocarpa* is present as large old monarchs at Itasca. In comparison, the mature bur oaks in the Waubun stand appear to be contemporary with the mature individuals of sugar maple and basswood. They are no larger than other species and lack the low branches and spreading crowns of open-grown trees. The largest tree of *Quercus macrocarpa* at Waubun is 22 inches d.b.h. which is smaller than most of the trees of that species in the Itasca stand. *Betula papyrifera* is present in both stands but it is not maintaining itself in the Waubun stand. Populus occurs in both stands but the species differ, *Populus tremuloides* being present at Itasca, and *P. balsamifera* at Waubun. Both species seem to have the same ecologic position in their respective communities.

The presence of the three coniferous species at Itasca and their absence from Waubun is one of the noticeable contrasts between stands. The position of *Abies balsamea* and *Picea glauca* is very different from that of *Pinus strobus.* As climax species of the northern conifer region the two former are shade tolerant, in contrast with the pine, and hence grow more successfully in the shade of the hardwoods.

Several other species of less importance occur in one or both stands. Ulmus is much more common at Waubun than at Itasca. Both *Ulmus americana* and *U. fulva* are present in the prairie margin stand, while only *U. americana* occurs in the Itasca stand. *Fraxinus pennsylvanica* is present in both stands but is of little importance. *Acer rubrum* and *Fraxinus nigra* occur at Itasca only.

Tree reproduction, especially of the dominants, is much more prolific at Itasca. There are eight and one-half times as many tree seedlings there and three times as many saplings as there are at Waubun (tables II and V). There are, however, some trees at both sites which are not effectively reproducing themselves. One is *Quercus macrocarpa,* which reaches the sapling class but then shows a gap to trees large enough so that their crowns reach through the canopy. The gap is especially pronounced at Itasca where there is nothing between small saplings and large old monarchs which rise well above the maple-basswood canopy. *Pinus strobus,* which is absent from the Waubun stand, is in the same situation at Itasca as *Quercus macrocarpa,* except that its seedlings do not even reach the sapling class. Other trees showing contrasting reproductive ability at the two stands are *Betula papyrifera* and the species of Ulmus. The birch is completely successful at Itasca as indicated by its presence in all size classes, but no individuals less than 2.5 inches d.b.h. were found in the Waubun stand. The elm is much more successful in the Waubun stand. *Populus tremuloides* at Itasca and *P. balsamifera* at Waubun occupy comparable positions. The data indicate fair reproductive capacity but actually what are listed as seedlings and saplings are root sprouts which do poorly in the shade of the forest.

The shrub layer also shows marked differences between the two stands. In contrast with the trees, the shrub flora is richer in species in the Waubun stand, there being 14 as compared with 9 species in the Itasca stand (table III). *Corylus rostrata* has the highest density in both places. The other species, however, which are common to the two stands do not necessarily make an equal contribution in both. While *Dirca palustris* and

Rubus strigosus are next to it in density at Itasca, it is *Ribes cynosbati* and *Prunus virginiana* that occupy this position at Waubun. In addition to a richer shrub flora at Waubun the shrub vegetation shows greater development there. In number of stems per unit area the Waubun stand has a greater density with 240 stems per 400 square meters compared with 180 for Itasca.

The herb layers of the two communities are so unlike that the communities look quite different. The Itasca forest is open and "grassy." The Waubun forest has a comparatively sparse ground cover. The difference in aspect largely results from the contrasting densities of the sedges at the two places. They are nearly four times as abundant in the Itasca stand. In addition the total density of herbs is over twice as great at Itasca. The two sedges are among the four most abundant species in both stands (table IV). *Uvularia grandiflora* also ranks very high in both. Only one other species, *Oryzopsis asperifolia,* is included among the ten most abundant species of both forests.

Some of the differences in the herb layers are striking. For instance, *Aster macrophyllus,* which is abundant and ubiquitous at Itasca Park, is so limited in the Waubun stand that only two plants appeared in the quadrats. Other species much more common at Itasca are *Galium triflorum, Maianthemum canadense* and *Rubus pubescens. Hepatica americana* and several others are of great importance in the Itasca forest but absent in the prairie margin forest. Table IV lists first the 10 most abundant species in order of decreasing density in the Waubun stand followed by the 6 remaining species of the 10 most important in the Itasca stand which were not included among the highest ranking species of the Waubun list. There is a total of 41 species of herbs at Waubun and 45 in the Itasca forest. Together they have a total of 63 species, which is somewhat over half the number, 104, listed by Buell and Wilbur (1948) for 10 hardwood forest stands of the area.

The amounts of light that get through the canopies of the two stands are very different. The value is 9.8 per cent at Itasca compared with 2.4 per cent for the Waubun stand. This difference in the amount of light is undoubtedly largely responsible for the marked difference in amount of reproduction and herbaceous ground cover in the two stands. It will be noticed that the low light penetration at Waubun does not prevent reproduction of *Acer saccharum* although it does greatly restrict it in comparison to the Itasca stand. Buell and Gordon (1945) reported that light penetration of less than 5 per cent prevents maple-basswood reproduction and ground cover from invading the spruce-fir forest. In view of the light data obtained from Waubun it seems likely that some factor or combination of factors other than or in addition to summer light intensity is operative. Factors to be considered are the evergreen habit of Abies and Picea resulting in year round deep shade, or possibly biotic inhibiting effects of the litter or the decomposing root sod.

The soil differences are likewise striking with a podzol profile at Itasca and a degraded chernozem at Waubun. The soil texture differs in the two sites, Waubun having a larger proportion of the finer fractions than Itasca.

4. Life-form spectra

Several life-form spectra were constructed using Raunkaier's life-forms (Raunkaier 1934). Four of these spectra are presented in table VII and along with them Daubenmire's (1936) spectrum of the Big Woods. The ones based on the flora (species list) show very little difference between the two stands. Spectra based on frequency points show much greater difference. Since they are so similar to those published by Buell and Wilbur (1948) they are not reproduced here. In these life-form spectra based on frequency points the emphasis shifts to-

ward the right of the spectrum when the Waubun prairie community is compared with the Itasca community. In other words the more protected life forms are more frequent at Waubun.

In an attempt to relate life-form dominance more closely to vegetation rather than to flora, further quantitative vegetation data were incorporated into the life-form study. The percentages of the various life-forms were figured using the total densities of each species (numbers of individuals per 2,500 square meters). Individuals were counted in the life-form in which they exist, for example seedlings of macrophanerophytes were counted as chamaephytes, etc. All individuals contributing to the communities were counted. This seems the most logical way of relating life-form to vegetation since a large number of individuals in the phanerophyte group may exist in the community in a suppressed condition, only a few getting beyond the layer in which we find them. For example in the Itasca stand, of nearly 30,000 seedlings of *Acer saccharum* which are existing as chamaephytes, scarcely 3 per cent live to function as microphanerophytes, as indicated by sapling density. Less than 0.07 per cent will become mesophanerophytes or mature trees. When the spectra are constructed on this basis the differences between the stands are even more pronounced than when frequency points are used. The second set of spectra in table VII shows what happens when this method of establishing a spectrum is used. A shift toward the right is evident if the Waubun spectrum is compared with the Itasca one. This method of using frequency and density values in weighting the various life-forms seems to be a more rational method for studying vegetation. Still better results might be obtained, however, if per cent cover or per cent of volume of the life-forms were used.

5. Comparisons with the Big Woods of central Minnesota and with the climax forests of Washburn County, Wisconsin

The Big Woods was the basis of a study by Daubenmire (1936). His methods were essentially the same as those used by the present authors. The Big Woods was originally the largest continuous area of maple-basswood forest in Minnesota. Its center, at the same

TABLE VII. *Life-form spectra.* Ch. = *chamaephytes*, H. = *hemicryptophytes*, Cr. = *cryptophytes*, Th. = *therophytes*

Based on flora or species list	No. of species	Phanerophytes				Ch.	H.	Cr.	Th.
		(Mega-)	(Meso-)	(Nano-)	(Micro-)				
Itasca	67		*32.8*			*3.0*	*46.3*	*17.9*	*0*
		(1.2)	(17.3)	(1.2)	(13.1)				
Waubun	62		*35.5*			*3.2*	*42.0*	*19.3*	*0*
		(0)	(12.9)	(1.6)	(21.0)				
Minnetonka woods (Daubenmire)	58		*22.0*			*14.0*	*29.0*	*33.0*	*2*
		(0)	(10.0)	(3.0)	(9.0)				
Based on density per 2,500 sq. meters	No. of individuals								
Itasca	145,186		*3.3*			*16.5*	*29.6*	*50.5*	*0*
		(.001)	(.08)	(.1)	(3.1)				
Waubun	83,960		*2.9*			*5.7*	*34.2*	*57.2*	*0*
		(0)	(.2)	(.3)	(2.4)				

latitude as Minneapolis, is about 2 degrees, 15 minutes (155 statute miles) farther south than Itasca. At the Maple Plain—Minnetonka woods area (about 20 miles west of Minneapolis) where some of the detailed studies of the Big Woods were made, the growing season is 44 days longer than that at Itasca and 32 days longer than at Waubun (Mahnomen). The precipitation is greater at Maple Plain (29.34 inches compared with 19.60 inches at Mahnomen, near Waubun, and 22.68 inches at Itasca). Higher summer temperatures at Maple Plain (the July average being nearly 6 degrees higher than at Mahnomen) together with the much longer warm season can considerably offset the effectiveness of the greater precipitation. (These climatic data are obtained from Climate and Man (Reichelderfer *et al.* 1941).)

In Washburn County in northwestern Wisconsin are maple-basswood stands which have been studied by Eggler (1938) in such a way that they also can be readily compared with those of the present study. The climate there is intermediate in length of growing season, average annual precipitation, and July average temperature between that of the Waubun area and the Minnetonka woods area, being somewhat more closely related to the Minnetonka area. Between it and Itasca Park the most pronounced difference is in the length of the growing season, there being 33 days less at Itasca, an amount sufficient to permit one to expect considerable difference in vegetation.

The principal dominants in the climax in northwestern Wisconsin, in the Big Woods of Minnesota, and in the Itasca-Waubun area are the same, *Acer saccharum* and *Tilia americana*. The phytographs constructed for these species by the various authors are strikingly alike in all three places. The presence of *Pinus strobus* in both the Itasca stand and the stands in Washburn County, Wisconsin, as well as the common dominance of the pines on the neighboring coarser soils seems to relate these two most closely. *Betula papyrifera* is another species that suggests a similar relationship between the northern Minnesota stands and the Wisconsin stands. Several species of a more general southern and eastern range suggest possible ameliorating effects of the climatic complex in Washburn County. These are *Quercus alba, Carya cordiformis,* and *Juglans cinerea* which do not occur in northern Minnesota; *Betula lutea* which occurs in the Itasca region only in the mature margin of bogs on peat soil; and *Carpinus caroliniana* which reaches its northwestern limit in the hardwood forests of the Itasca region, although it is absent from the stand studied and uncommon elsewhere in the region.

In the same way the Waubun stand lying west of the conifer region of Minnesota is similar to the Big Woods. *Betula papyrifera* and *Populus balsamifera,* absent from the Big Woods, are two tree species of the Waubun stand that reflect its proximity to the northern conifer forests. *Carya cordiformis* is the one tree species of the Big Woods that does not occur as far north as Waubun. *Quercus borealis* var. *maxima* does grow in the vicinity of Waubun though not in the stand studied. *Celtis occidentalis* grows on flood plains at the latitude of Waubun. Both species are in the maple-basswood climax forest of the Big Woods.

Likewise certain shrubs and herbs whose principal area is south and eastward are found in the Big Woods and in the Washburn County woods. *Hamamelis virginiana* in the Wisconsin woods (but not in the Big Woods of Minnesota in this case) is one of these. Also certain species that occur in the Big Woods, such as *Sambucus pubens* and *Zanthoxylum americanum,* grow only in more open places in the north. Apparently in the north they can tolerate less shade or competition. There are, however, more species of shrubs in the Waubun woods than in either the Minnetonka or the Washburn County woods

(13 compared with 9 and 10, respectively). The same is true of herbs with 41 at Waubun, 31 at Minnetonka and 35 in the Long Lake stand in Washburn County. These numbers are based on the same areas sampled. A very appreciable difference exists between all stands in the species of herbs having highest density. Among those which contribute most, *i.e.,* the first 10 in each case, *Carex pensylvanica* is the only one common to all of them. Altogether there are only 9 herb species common to the 4 stands. The Waubun stand is beyond the range of some of the herbs like *Mitella diphylla* and *Geranium maculatum* which are in both the other two areas. Most of the herbs listed for the Big Woods and Washburn County woods occur in the vicinity of the Itasca or Waubun forests but are absent from the stands studied. Occasionally, like the shrubs mentioned above, an herb is absent from the maple-basswood forest in the north, apparently being restricted by its intolerance to shade at that latitude. *Smilax herbacea,* for example, of the Minnetonka woods is a species which seems to demand more open sites at the latitude of Itasca.

The stature of the Waubun forest is intermediate between that of the extreme eastern and western limits of the Big Woods, and this fact is suggestive of the possible relation between the position of the Waubun forest and the climatic limit of the community. In height the Waubun forest with an average of 65 feet is inferior to the best development of the Big Woods which Daubenmire measured and found to be about 89 feet. It is also below the average height of the Big Woods. It does exceed, however, the 51 foot measurement of the Big Woods at its western limit. Daubenmire believed that the 51 foot height attained by trees on the forest margin suggested that climate is not limiting their westward extension, *i.e.,* that potentially they could grow and mature farther west. If that is true the same argument may be raised for the forest at the latitude of Waubun where the prairie margin stand is 65 feet high.

The life form spectra of the Waubun stand and the Minnetonka stand of the Big Woods can be compared since Daubenmire constructed such a spectrum. Both are presented in table VII. A greater emphasis toward the right hand end of the spectrum is evident when that of the Minnetonka woods is compared with that of the Waubun woods, that is, the proportion of the more protected life-forms is greater. To the extent that life-form spectra based on species lists of communities can be relied on as climatic indicators this suggests a pronounced climatic difference between the areas. One might infer from the life-form spectra that the climate is somewhat more rigorous for native vegetation at the Minnetonka woods than in the region to the north. On the basis of the climatic data this does not seem probable. It would be desirable to have life-form spectra based on quantitative data for such comparison.

Discussion

History of the stands

The information which we now have on the two stands specifically and for the region in which they lie makes it possible to a certain extent to reconstruct the vegetational history of the area. One can also find in the data evidence that gives a clue to the possible cause of the recognized past vegetational changes. There are two alternatives, fire and climatic change; each has some support in the evidence. Although both factors may have been acting equally and together, there appears to be somewhat greater weight of evidence in support of climatic change as the predominating cause.

The present structure of the communities and the features of the underlying soil profiles both contribute evidence concerning the history of the stands. This evidence is strengthened by studies of soil-vegetation relationships made elsewhere along the prairie-forest ecotone as well as by reconstruction of post-glacial

vegetational history based on pollen spectra of bogs in the vicinity.

The Itasca stand shows evidence of having changed from a community in which *Pinus strobus* and *Quercus macrocarpa* were more important, to the present mesic community dominated by *Acer saccharum* and *Tilia americana*. The existing trees of both *Pinus strobus* and *Quecus macrocarpa* are all large, old specimens reaching above and greatly antedating the younger maple and basswood elements of the community. No new individuals of these species are being added to the community, due to failure of seedlings to mature. This has been true for some time.

A succession similar to that which led to the situation now existing in this stand can be seen in process in adjacent areas today. In fact one can find several places in Itasca Park where stands of white pine or mixed white and red pine (*Pinus resinosa*) are being replaced by the maple-basswood community. Kittredge (1934) found the same succession taking place on Star Island in Cass Lake about 30 miles northeast of Itasca Park. The hardwood stand on Star Island he believes to be three hundred or more years old. The community is now in the process of spreading out and displacing the pine communities. This probably represents the type of succession that has been going on in northern Minnesota for some time. Within this region the number of habitats in which the hardwoods have been able to displace the pines appears to have increased. The area over which the hardwoods can exert the dominating influence is such that most workers in the region have considered them as forming the climax community. Potzger (1946) finds that this replacement of pines by hardwoods has taken place since the xerothermic period in northern Minnesota, Wisconsin and Michigan. On the basis of the few pollen spectra available for the vicinity of Itasca Park, Potzger's (1946) figures 15 and 16 and Erdtman's (1943) figure 11, the change is very recent, more so than for farther east. The change from pine to hardwoods is not evident in Potzger's profiles from Hubbard County, adjacent to Itasca Park, but a reduction of pine does appear toward the top of Erdtman's profile which is from a bog in Itasca Park.

Aside from the present obvious trends and the supporting evidence for these trends from the pollen history, there is little other evidence of recent change. The pronounced podzolic profile of the soil, while not necessarily positive evidence, certainly is not out of harmony with the theory of a long pine period ending in very recent time.

The Waubun stand also is suggestive of recent vegetational change. In this case there has been a succession from prairie climax to the maple-basswood climax. The evidence comes from two sources, the structure of the vegetation and profile characteristics of the underlying soil.

The absence of large, old monarchs of an earlier generation of forest cover is noticeable. Although there are some large elms in low places peripheral to the maple-basswood community there are, in the stand, no old trees with large, spreading branches suggesting that they grew in the open. The ground is even, there being no mounds and holes such as are produced by decay of uprooted trees or old root systems of generations past. In fact the forest has every appearance of being a first generation which has invaded en masse a previously unforested area, either a prairie community or a shrub community that had become established on prairie. On the basis of ring counts of a few cut stumps available, the mature trees appear to be 130–140 years of age. This suggests an approximate date for the invasion.

Study of the soil profile seems to support the theory of a recent forest invasion of the prairie at this location. Superficially, along a road cut the profile looks like a true chernozem. Also on closer

examination a well developed crumb structure and black color are found to be present in most of the A horizon. The most pronounced peculiarity of the profile is the podzolized upper 3 centimeters of the A horizon. This leached layer has a marked gray color and platy structure. Not only is this modified profile evidence of the occupation of a former prairie by forest, but the forest being in the neighborhood of 130–140 years of age suggests the rate at which a prairie soil may undergo podzolization in this region. Under other situations the process of podzolization is slower (Kittredge 1929, Chandler 1942). This may indicate that this forest is further behind its climatic limit than marginal forests at other localities.

Supporting the idea that the Waubun forest represents an invasion of prairie in recent time are reports by numerous authors of similar changes elsewhere. Ewing (1924) working in the same county recognized recent westward advance of the forest. Aikman (1928) described a dynamic situation in the ecotone between prairie and woodland in southeastern Nebraska where the forest is the aggressor. McComb and Loomis (1944) and Loomis and McComb (1944) found several advances of forest in Iowa which occurred at several times in the past, some earlier, some later than the time the Waubun forest was established. Moss (1932) found that the aspen parkland invaded the black prairie soils in Alberta. He believes that "groves of trees have been abundant in the greater part of the parkland for many years but not for centuries" since the black soils on which the woodland is growing show "only a slight transformation of the kind expected in grassland soils that have been wooded for many centuries." Brink and Farstad (1949) reported a similar recent advance of aspen forest followed by lodgepole pine and spruce into grassland in the intermountain valleys and plateaus between the Coast Range and the Rocky Mountains in northern and central British Columbia. They based their conclusions both on records of early explorers and on the degradation of black grassland soils now occupied by woodland.

Cause of the succession

There are at least two possible causes for the successions, for both of which there is some supporting evidence. One is the past influence of fire on the vegetation. Fire could have been responsible for maintaining pine forests in the Itasca region and for favoring prairie over forest far to the east of the potential climatic boundary. The relatively recent release from forest fires due to the influence of settlement by white man may have favored the recent successions. Another possibility is a change in climate to a moister regime which has favored these successions in the two areas. It is of course possible that both factors could have operated togethor since a moister climate would also be less favorable to fires. Furthermore it is likewise possible but perhaps less likely that it could have been the climatic factor operating at one place and the pyric factor operating at the other.

Forest fires have entered the Itasca stand. Large fire scars are present on all the pines. However, there have been no recent fires in the park and, as mentioned above, there is evidence of continuing expansion of the Acer-Tilia community into an adjacent pine stand, a pattern repeated in other places throughout the region. The situation could easily have resulted from recovery from a period when ravages by forest fires were frequent and often severe. If this is what has happened, the questions arise as to where and how the elements of the Acer-Tilia community lived through the ravages of the fire period, and why there was such a change in fire incidence. The older stand of maple-basswood that forms the basis of this study at Itasca Park does not occupy a site that is naturally a refugium from fire as it might if it were sheltered, as many such communities are,

on the lee side of a lake for example. It has only rolling morainic hills to the west of it, not too effective a break to conflagrations moving before the west winds.

It is of course quite conceivable that the older pines and bur oaks came in after a very severe burn opened up the area and that Acer and Tilia and their associates were slow to return to this spot from some refugium and even slower to spread from it. If the succession from pine to hardwoods began with the establishment of the hardwood communities that are the subject of this paper then the change in fire practice came before the period of settlement. It is difficult to see why there should have been a change in fire protection at so early a date. Nevertheless, whatever the absolute role of fire may be it is obvious that it cannot be disregarded as a very important factor in influencing the forests at Itasca Park in relatively recent time.

Similarly fire has not been absent from the stand at Waubun but the thick layer of humus on the ground indicates that the woods has been free of it for a considerable period. That fires were common at least around the beginning of the century is certain since the older residents report them. The farmer who owns and cultivates the large field just west of the Waubun stand reported that when he first came there about 1900 this field was brushland similar to some of the adjacent land at present. He said that fires burned through the brushland very commonly. They must certainly have entered the Acer-Tilia stand at times as there was no barrier to prevent them.

Aside from this there is nothing at the site that suggests that the western margin of the forest is a fire-held line. It is, however, true that other workers studying the tension zone farther south have found that prairie fires are responsible for maintaining the forest-prairie margin where it is at present. Daubenmire (1936) has shown by plotting the western limits of the Big Woods that rivers and lakes play a large part in determining this boundary. Such bodies of water and water courses make good fire breaks. The forest outliers are groves of the more fire-resistant *Quercus macrocarpa* which occur west of the margin of the Big Woods. Similarly in southwestern Wisconsin such outlying groves of oaks, known as "oak openings," were quite characteristic at the time of the early land surveys. Cottam (1949) believes that they represent a fire controlled community. Within the last 100 years, with reduced fires, *i.e.,* during the period of settlement, these "oak openings" have become closed forests and the less fire tolerant climax species such as *Acer saccharum* and *Tilia americana* which were never mentioned in the early survey records are now entering into the new forests. The evidence is rather convincing that fire has been a factor in governing the location and character of the prairie-forest margin in both of these places. Several students working in the "prairie peninsula" of Illinois, Indiana and Ohio have found fire-maintained prairie under what appeared to be a forest climate, although Transeau (1935) has shown that the "peninsula" has some prairie climate characteristics. Such evidence as has been cited by Daubenmire (1936) for fire controlled prairie-forest margin and as cited by Cottam (1949) for the fire controlled succession of oak opening to deciduous forest do not seem to be present in the area studied. This is not proof, however, that fire has not played an important role in influencing succession in the two stands. It can merely be stated that there must have been fires that undoubtedly affected the community to some extent in the past.

On the other hand, as mentioned above, there is the possibility that the succession is a response to climatic change. This possibility is supported in the Itasca area by pollen profiles. The dominance of pine during so much of post glacial time when Acer and Tilia have been scarcely if at all represented suggests that pine forests may have been more

than fire subclimax. It is more indicative of a long period during which pine was continuously dominant and self-perpetuating in most of the habitats. The pollen spectra from farther east—Potzger's (1946) figures 19, 22, 23 and 24 from Wisconsin for example—indicate that the change from the pine dominance occurred much earlier in post glacial time. There seems to be little doubt that this latter is the result of climatic change. What the evidence of forest succession in northwestern Minnesota may indicate, then, is a shift over from pine forests to a hardwood climax as a result of a moister climatic regime, similar to that occurring earlier farther east. That the shift is later here may be due to the drier and more continental climate of this region. Although the pollen record is very suggestive of this there appears to be but meagre evidence in today's vegetation in this region to indicate that pine can be climax. It is only on coarse, sandy soils that the pines are able to perpetuate themselves. Is it too presumptuous to suggest that more xeric climatic conditions might in the future induce or in the past have allowed them to spread out from these restricted sites and become aggressive on what now are the most mesic sites? Whether we should give the extensive pine forests that appear to have occupied much of this region for so long a period climax status is a matter for speculation. Perhaps it could have been a long existing successional stage although the time interval seems excessive.

That the forest advance onto the prairie at Waubun is the result of climatic change has several sources of support. One is the soil profile development. Another is the apparent time of the last main advance of the forest onto the prairie. Another is the extensiveness of the phenomenon around the periphery of the northern grasslands. Furthermore the absence of strong evidence for fire as the principal control lends favor to a climatic explanation.

The soil profile at Waubun has already been described. As a degraded chernozem soil it at once suggests the former occupation of the area by grassland followed by forest invasion. The three centimeters at the top of the A horizon in which the soil is gray in color compared with the black of the rest of the horizon is excellent evidence for the occupation of the land by the forest under a forest climate. Not only does it show a color change but a distinct structural change has begun to take place from the typical crumb structure of the grassland soil to a platy structure. Podsolization suggests both climatic and vegetational change.

Similar occurrence elsewhere of forest invasion of grassland has already been mentioned. In some instances it may have been due to reduced incidence of prairie fires. This is especially true farther south where settlement was earlier. The widespread occurrence of forest invasion of grasslands in the north as indicated by the work of Moss (1932) in Alberta and Brink and Farstad (1949) in northern and central British Columbia lends more support to the theory of climatic change as an explanation of the phenomenon than the theory of change in fire incidence.

This is especially true when the apparent time of the forest advance is considered. It has already been shown that the Waubun forest was established about 1810. Moss could not trace the aspen parklands back beyond about 1818 since *Populus tremuloides* is a comparatively short-lived tree. He did say, though, that the degree to which the soil profile has been modified by the woodland vegetation suggests that the aspen has been on the prairie soil "for many years but not for many centuries." The year 1810 in northern Minnesota and a similar or somewhat earlier year in Alberta antedate the settlement of these regions by white men. Hence any possible reduction of fire incidence at that time must be explained by some change other than white occupation. It seems doubtful that the

Indians would have changed their practice in regard to prairie burning about that time. Since white settlement was so much earlier farther south the argument becomes less convincing there, but it is interesting to note that McComb and Loomis (1944) found expansion of hardwoods at the expense of prairie to have occurred previous to the time of settlement in Iowa. In addition it should be pointed out that fires were common in the Waubun area as recently as the early years of this century, long after the establishment of forest on the prairie there.

The Waubun stand has every appearance of having started as a unit. It suggests mass invasion of the open upland, possibly from the streambank woodlands. There are other stands in the vicinity that appear to be of similar origin. There is not, however, a series of maple-basswood stands representing various successive ages from this mature forest on down to very young trees and extending successively westward as if the community had been gradually spreading out along a broad front. The forest stands give the appearance of having spread rapidly at a time of especially favorable climatic conditions, Since then, the environment has been favorable enough for the community to hold territory it had gained but not favorable enough for further invasion of established prairie or brushland. The westward advance of the forest thus shows an uneven method of progression, very suggestive of what Conway (1949) has found in the bogs of this region: "phases of rapid extension in area of a vegetation type, separated by intervals of less or no extension, but of consolidation and maturation." The bogs are more sensitive recorders of minor climatic fluctuations in which 40- or 50-year intervals are dectectable. The forest margin would respond only to larger climatic cycles when periods of greatly improved water balance make possible forest invasion of prairie or marginal brushland. At such a time the forest moves out rapidly as a great wave. In speaking of vegetational response to climatic change Conway (1948) says: "Thus any particular type will have a range of tolerance in regard to climate, and will not change unless the climate changes beyond the threshold of tolerance. Hence, any particular alteration of the local resultant climate—need not be expressed at all by the vegetation of that locality." In the ecotone between forest and prairie, resistance to invasion of one by the other is sufficient, so that a swing in climate must go well beyond the minimum climatic requirement for the existence of the community to effect a change from one climax to the other. Hence, it is a matter of reaching a threshold beyond which forest can invade prairie. Although cyclic climatic changes have doubtless been long in effect along the forest-prairie boundary, only at ocasional points in time and in space have pronounced forest advances been possible. At Itasca Park, on the other hand, continued succession from pine to hardwoods may possibly suggest that there a threshold was reached and subsequent climatic fluctuations have not again permitted pine dominance.

The conclusions appear on the surface to be out of harmony with the record of glacial retreat in Alaska as well as elsewhere. Yet, although the glaciers have in general receded since about 1765, there have been halts and minor advances as indicated by recessional moraines suggesting brief periods favorable to glacial growth (Lawrence 1950). Furthermore, there is evidence of unusual weather occurring in eastern North America in the early nineteenth century. Moseley (1941) stated that according to records Marietta, Ohio ". . . had almost double the usual amount of rain in September, October, and November 1822. The tree rings formed in 1822 and 1823 indicate that more rain fell in those years than in any two previous years in the century." Kincer's study of the weather records indicates an especially cold period in the early eighteen hundreds. Basing his figures on 20 year moving temperature sum-

mations for New Haven, Connecticut, which has the longest records for the United States, he found a pronounced low temperature period around 1825–30. Humphreys (1920) mentions the unusually cold weather following eruption of several famous volcanoes between the years 1812–1815. For example, 1816 was known as the "year without a summer," "poverty year," or "eighteen hundred and froze to death." It was cold the world over. None of these, of course, proves anything about the climate of northwestern Minnesota. They do, however, suggest that a climatic swing favorable to the invasion of prairie by forest may reasonably have been expected somewhere around 1812–1825. It should also be emphasized in closing that the Waubun stand is at the western edge of the deciduous belt. For several miles to the east of it black soils are occupied by the hardwood forest. Casual observation makes it appear quite probable that further field studies will reveal evidence that earlier and more extensive invasions of prairie by forest have occurred.

Summary

1. Two communities dominated by *Acer saccharum* and *Tilia americana* are described and compared. The communities are at the same latitude and but 30 miles apart. One is near Waubun, Minnesota, at the margin of the prairie. The other is at Itasca State Park in the hardwood-conifer forest tension zone. Comparisons are also made with the maple-basswood forests of southern Minnesota and northwestern Wisconsin.

2. Evidence based on community structure and soil profile indicates that the maple-basswood forest has recently invaded prairie en masse.

3. Evidence is also presented which indicates that the maple-basswood community at Itasca Park has succeeded a pine-oak community. It is based on community composition and structure and on available pollen analyses of bogs in the region.

4. The two most likely causes for these successions, fire and climatic change, are evaluated. While it is recognized that both have played an important part, it is considered that climatic change has been the principal controlling factor.

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NATURAL BREEDING SITES FOR SOME WILD SPECIES OF DROSOPHILA IN THE EASTERN UNITED STATES

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In the body of literature which deals with flies of the genus *Drosophila,* there is an increasingly large and significant segment which is concerned with the genetics of natural populations and in which special attention has been given to the study of problems of speciation and microevolution. Purposely chosen for much of this type of work have been those species of the genus which appear to be ecologically the least affected by the activities of man and which are generally considered "non-domestic" or "wild" [1] species. Thus, in the western United States, attention has been centered on such wild species as *Drosophila pseudoobscura* and its relatives (*e.g.,* Dobzhansky and Epling 1944), whereas in the eastern and south-central parts of the country such forms as *D. algonquin* (Miller 1939), the *americana-texana-novamexicana* complex (Hsu 1950) and *D. robusta* (*e.g.,* Carson and Stalker 1947) have been used.

In contradistinction to the clearly domestic species, which are mostly cosmopolitan in distribution (*e.g., D. melanogaster, D. hydei, D. immigrans, D. busckii* and others), the so-called wild species are most readily trapped in relatively undisturbed woodland habitats and have discontinuous and natural distributions. These species, furthermore, are only rarely bred from garbage, rotting fruits, vegetables and similar potential breeding sites associated with the activities of man. This does not mean that the distribution of wild species is totally unaffected by human activities because, with some exceptions, the members of the genus are generally adaptable and will be attracted to, and feed upon, any carbohydrate source which permits the growth of yeasts. Althuogh varying degrees of difficulty are encountered, many of the species of *Drosophila* may be reared in the laboratory on commercial yeasts; customarily all that is required is a carbohydrate source sufficient to support the growth of yeast and which also assures the maintenance of proper humidity conditions in the culture.

The above facts suggest that yeasts, as well as associated bacteria and related micro-organisms, form the principal food material for both adults and larvae of many species of the genus. That adults of wild species do feed on such materials in nature may be easily demonstrated by dissecting and examining the crop-contents of wild-caught flies which have had no direct contact with the baits used to attract them. On the other hand, it is clear that the wild species do not breed indiscriminately or abundantly on domestic materials, even though they may readily feed upon them if presented with the opportunity. These facts, together with the repeated observation that very large numbers of flies belonging to wild species can be easily captured in woods far from human habitation, indicate that naturally-occurring carbohydrate substrates must constitute the principal breeding sites for these species.

Very little information is available on breeding sites for wild species; published data are, in the main, fragmentary and are satisfactory only for a few species which breed on fleshy fungi and for several which breed in certain specialized locations, as, for example, *D. mulleri* and and its relatives, which have been found to breed on the fruit of the cactus, *Opuntia lindheimeri* in the southwest (Wagner 1944).

The importance of detailed information on the fundamental ecology of certain

[1] See Patterson and Wheeler (1942) for a discussion of this terminology.

species, especially those on which studies of population genetics have been made, is very great. For instance, seasonal cycles in the incidence of certain chromosomal arrangements and geographical gradients of morphological and cytological characteristics have been described in some of these species. The principle of natural selection has been employed in the interpretation of these phenomena despite the fact that there is very little indication as to what the nature of the selective forces is, especially during larval and pupal life. Knowledge of breeding sites might also permit more refined methods of obtaining samples of natural populations. Almost without exception, specimens on which studies of natural populations of *Drosophila* have been made were obtained by placing traps containing fermenting fruit (almost exclusively banana) in the woods. The drawbacks of such a procedure are obvious. In the first place, there is no assurance that the population sample attracted to a tropical fruit placed artifically in a temperate forest is a random one. Secondly, such baits may result in an abnormal concentration of flies around the traps; this makes the determination of the vital factor of population size an extremely difficult one. Thirdly, the specimens obtained in this way represent a sample of the adult population only, as the collection of population samples of larvae and pupae has only rarely been possible. These adult samples, finally, may not always represent a sample of the true breeding population, either because of a possible differential attractivity of baits and natural breeding sites or because certain of the flies captured may not be in active reproductive condition. As an example of the latter, we have demonstrated, by dissecting wild flies caught in banana traps, that the fall populations of *Drosophila robusta* are non-breeding, the females, at least, being mostly uninseminated and in a state of reproductive diapause (Carson and Stalker 1948).

The data to be presented in this paper represent the outcome of concerted efforts to locate the breeding sites of certain of the species of *Drosophila* native to the woods of the eastern United States. Particular attention has been given to *D. robusta,* inasmuch as it has been used extensively by us in previous studies of cytological and morphological variation.

Procedure

Over the years 1946 to 1948, we have made extensive collections of Drosophila in the vicinity of St. Louis, Missouri. The large bulk of these collections was made with the use of traps, baited with banana or other fermenting fruit and placed in deciduous woodland. In addition, a considerable number of individual flies have been collected when observed in natural situations and a small amount of net sweeping has been done.

In collections from banana traps set in woodland, we have recorded a total of approximately 48,000 individuals of the genus, belonging to 28 species (table I). Of these species, seven are clearly domestic in habit (Groups IV, V, and VI); the remaining twenty-one (about 35,000

Table I. *Species of Drosophila recorded in woodland collections from banana traps during 1946, 1947 and 1948 near St. Louis, Missouri. All the collecting was done in a single deciduous woods (Olivette Woods). In each of the six groups, the species are listed in order of their relative frequency in banana traps*

	Generally common during June and July (1% or more in trap collections)	Rare; local; common at other seasons; or not well attracted by baits	
		Less than 1% during June and July	Not captured during June or July
	I.	II.	III.
Wild Species (21)	*athabasca* *robusta* *melanica* *affinis* *nigromelanica* *algonquin* *putrida*	*transversa* *tripunctata* *testacea* *duncani* *macrospina*	*narragansett* *alabamensis* *victoria* *americana* *colorata* *quinaria* *sigmoides* *guttifera* *pseudoobscura*
	IV.	V.	VI.
Domestic Species (7)	*immigrans* *melanogaster*	*hydei* *simulans* *funebris*	*busckii* *repleta*

individuals) are considered wild species. Of these species, however, only about seven (Group I) are generally common in banana traps during June and July, the time at which the principal observations reported in this paper were made. It should be stressed, however, that the criterion of abundance used here, the relative number of flies attracted to baits, may be a somewhat misleading one. A number of species are obviously only mildly attracted to such traps or enter them only by chance. Future investigation may reveal that a number of species are actually locally, or even generally common. Nevertheless, evidence from all types of collections indicates that, in this vicinity and at this season at least, these seven are the most generally abundant. Accordingly, the location of breeding sites for these species has posed itself as the primary and most easily approached problem.

The field studies and collections presented here were made mostly without the use of baited traps and cover principally the months of June and July, 1948 and 1949. June, and probably also the month of May, appears to be the height of the breeding season near St. Louis for *Drosophila robusta*. Beginning about the middle of June, a considerable proportion of the flies of this species captured in banana traps are lightly-pigmented and have obviously recently emerged from the pupal case. As the development from egg to emergence of this species takes 16–17 days in the laboratory at 25° C. and approximately 28 days at 17° C., the eggs from which these young flies developed must have been laid in nature in late April or May. Investigation of the problem of breeding sites, especially for *D. robusta* and certain of the *affinis* group, is best carried out early in the year when large quantities of flies are hatching in the woods, well before the domestic gardening and fruit-ripening season has begun. It is thus possible to effectively minimize the competition between natural and domestic breeding and feeding sites which may become an important factor later in the year.

In the eastern deciduous forest, three major types of carbohydrate sources suggest themselves as possible substrates for the growth of micro-organisms which could in turn support larvae of *Drosophila*. These are: (1) native wild fruits, flowers, nuts and nut hulls, (2) fleshy fungi, especially those which deliquesce and do not desiccate rapidly, and (3) sap exuding from trees or other woody plants. Intensive searches in the field were made for objects in each of the above categories which might support the growth of *Drosophila*. In many instances, fresh or decaying fungi were marked and visited repeatedly at varying times of day and under varying weather conditions. Records of observation of the behavior of any species of *Drosophila* found regularly frequenting such materials were made in the form of protocols.

A large number of collections of materials considered likely to contain *Drosophila* eggs, larvae or pupae were made; these were brought to the laboratory and immediately searched for the presence of immature stages. If such were found, in many cases these were transferred to vials containing standard cornmeal-Karo-agar medium which had been inoculated with fresh Fleischmann's yeast. Although it is by no means certain that all species of *Drosophila* may be successfully transferred in this way, the method proved to be valuable for most of the species found. The remainder of the specimen was then plated out on either sterile or yeast-inoculated medium in vials or milk bottles, although in some instances the material was placed *in toto* in an empty, clean glass bottle or vial. It was found, however, that the maintenance of proper humidity and physical culture conditions in the laboratory is difficult unless a small amount, at least, of medium was present in the culture. Cultures prepared in this way were then observed over a period of several weeks and emerging species of *Drosophila* and other Diptera recorded.

Observations

Native wild fruits

The deciduous forest of the eastern United States has a notable lack of fleshy fruits which could serve as important breeding sites for wild species of *Drosophila,* especially during the spring and early summer. Not only are most of the fruits small (*e.g.,* mulberry, hackberry, wild cherry, blackberry, wild grape, etc.) and not only do they desiccate rapidly as decomposition sets in, but most ripen well after the population of many species of *Drosophila* has been built up. It is probable that later in the season certain of these fruits serve as breeding sites for some of the smaller species, but because they are obviously not the answer to the primary question they have not been systematically examined.

We have reared both *Drosophila affinis* and *D. tripunctata* from rotting fruits of the may apple (*Podophyllum peltatum*) collected during the third week of July. A few specimens of *Drosophila athabasca* were reared (along with many individuals of the domestic species *D. melanogaster* and *D. simulans*) from rotting persimmons (*Diospyros virginiana*) collected shortly after falling, in the middle of October. These records, however, are relatively quite late in the breeding season and represent fragmentary observations. Sturtevant (1921) mentions having reared *affinis* from huckleberry, and Malloch and McAtee (1924) have bred *D. melanica* from butternut hulls.

Fleshy fungi

Fleshy fungi, especially large agarics, provide natural breeding sites for a number of species of *Drosophila* (Sturtevant 1921, 1942; Spencer 1942). During the present study, we have repeatedly bred *D. tripunctata* and *D. transversa* from a wide variety of fleshy fungi; this is in accord with the earlier observations of Sturtevant (1921) and Malloch and McAtee (1924). There seems to be no record of *transversa* from domestic sources, but *tripunctata* is apparently less restricted, as we have bred it from pumpkin and the above authors record it as breeding in cabbage, banana, watermelon and squash. Both of these species may be considered rare in this locality during June and July; their population peaks, as indicated by banana trap captures, appear to occur during late summer and early fall. The related species *D. putrida* has also been bred from fungus, but not as consistently as the two species mentioned above.

Efforts were made to survey as wide a variety of fungi as possible, in the hope that certain forms might be found suitable for the development of other wild species, such as *melanica, robusta* and the *affinis* group. Although *melanica* has never been observed near fungi, both *robusta* and the *affinis* group were repeatedly seen feeding on deliquescent specimens, and for this reason extended field observations and collections of fungi were made. Despite these determined efforts, however, we have only a single record of *D. robusta* breeding on fungi; in this case flies were reared from a deliquescent cup-fungus collected late in July. In only two cases were we successful in rearing any member of the *affinis* group from fungi; these were determined as *D. athabasca.* The above instances, although they are the first records of these species breeding on fungi, appear to be exceptional in view of the large number of fungi examined and the apparent large population of these species present in the woods at the time the study was made.

Sap exudations from trees

During the 1949 season, particular attention was given to the study of exuding tree sap as a possible breeding site for *Drosophila.* The flow of sap from a tree is known as fluxing, and may be observed in a wide variety of tree species. Fluxing may apparently have any one of a number of basic causes, ranging from injuries caused by boring insects or frost cracks, to an actual bacterial infection

of the heartwood, as in wetwood disease of elms (Carter 1945). Whatever the basic cause, the sap, as it emerges on the surface of the branch, trunk or exposed roots of the tree, may become infected with various micro-organisms, including yeasts, bacteria and molds. Such a condition has been referred to as a "slime flux."

It has been known for some time that a number of species of *Drosophila* are attracted to and will feed upon exuding sap. Records of breeding, however, have been only occasionally reported, and no serious survey has been made. Sturtevant (1921) records *D. tripunctata* breeding on the sap of a bleeding grapevine and further remarks that *D. affinis* is "not rare about bleeding trees." He also mentions an observation of *D. melanissima,* a species not found in the St. Louis area, which was present "in large numbers about moist sawdust made from a living pine by a boring beetle." Malloch and McAtee (1924) state that *D. colorata,* a woods species closely related to *robusta,* feeds on sap in both the larval and the adult stages. Patterson and Wheeler (1942) emphasize that *D. victoria* is common around the sap of bleeding cottonwood trees; Sturtevant (1942) has suggested that Malloch may have recovered larvae of this species from a similar location. With respect to *D. pseudoobscura* and *D. persimilis,* Dobzhansky and Epling (1944) cite two instances in which these species were found breeding in sap in California. The host species involved were a wild grapevine (*Vitis californica*) and the exotic tree, *Cedrus deodara.* Gordon (1942) has found both *D. subobscura* and *D. obscura,* which are

TABLE II. *Species of Drosophila breeding on slime fluxes near St. Louis, Missouri, June and July, 1949*

Host species	No. of fluxes cultured	No. of fluxes positive for *Drosophila*			Species other than *robusta*
		All species	*D. robusta*	Other species	
INDIGENOUS					
American Elm (*Ulmus americana*)	23	6	5	1	*victoria*
Slippery Elm (*Ulmus fulva*)	27	6	5	1	*victoria*
Wild Cherry (*Prunus serotina*)	5	2	2	0	—
Red Oak (*Quercus borealis*)	6	1	1	1	*melanica; athabasca*
White Oak (*Quercus alba*)	6	1	1	0	—
Pin Oak (*Quercus palustris*)	6	1	1	1	*repleta*
Red Mulberry (*Morus rubra*)	5	3	3	0	—
Black Willow (*Salix nigra*)	7	1	1	0	—
Cottonwood (*Populus deltoides*)	6	1	1	0	—
Black Locust (*Robinia pseudo-Acacia*	3	1	0	1	*melanica*
INTRODUCED					
Chinese Elm (*Ulmus parvifolia*)	5	2	2	2	*melanica; victoria*
Garden Plum (*Prunus domestica*)	1	1	1	0	—
Peach (*Prunus persica*)	4	3	3	0	—
White Mulberry (*Morus alba*)	6	1	1	0	—
Totals	110	30	27	7	

FIG. 1. A breeding site of *Drosophila robusta* at the base of an American Elm. The extent of the area of slime flux is indicated by arrows.

wild species in Britain, feeding on exudates of elms. In one instance, *D. obscura* was reared from such an exudate. In view of the fragmentary nature of these observations, none of the above investigators, with the exception of Gordon, has suggested that such locations represent important breeding sites.

For a period of about six weeks from early June to the middle of July, 1949, sap exudations, both with and without slime flux, were examined. Such fluxes were not only found to be abundant on a large variety of trees, but also to present considerable and puzzling variability. Thus, some slime fluxes of elms were light brown in color and had a gritty, watery consistency; in others, the slime flux was soft, dark brown and somewhat glutinous. In still others, a yellowish-white, sponge-like mass, saturated with actively flowing sap, was found. Fluxes of other species of trees showed similar variations in the qualitative consistency and appearance of the slime flux. Variations with time were also evident. Some spots were found in which the sap was running or bubbling out of the trunk on one day, only to dry up without the formation of slime flux several days later. In some, diurnal periodicity of flow was observed; in others, the areas appeared essentially unchanged over a six-week period. No serious attempts were made to classify or to study the micro-biology of the sap exudations under observation.

The method of study consisted of macroscopic examination in the field for presence of suggestive-looking pupae or larvae as well as collection of samples of the flux, if the place seemed capable of supporting *Drosophila*. Detailed notes of all adult *Drosophila* found near such places were kept. Cultures were followed and emerging species recorded (table II).

D. robusta was reared from 27 sites on 12 species of host trees, 8 of which are native to the Missouri woods. Although the fluxes cultured were originally selected as "likely-looking," a number of

them were negative and remained so, even upon repeated attempts to breed *Drosophila* from them. The explanation of this probably lies both in the fact that many slime fluxes were located in exposed suburban or park-like areas where *D. robusta* is not abundant and in the variety of unknown factors which underlie the extraordinary variability in the physical, and presumably the microbiological and chemical, nature of the slime fluxes. After several weeks of study, it was apparent that *Drosophila* was most commonly associated with brown slime flux which was soft and smooth, with a consistency varying between that of cottage cheese and mayonnaise. The small number of cultures made from certain tree species (*e.g.*, Plum), and the small number of positive cases for certain host species (table II), reflect the tendency which was followed, to obtain as many different host species as possible, rather than build up data on any individual

FIG. 2. Habitat view of rather open woods. *Drosophila robusta* was bred from slime flux which had developed in the scar of the American Elm indicated by the arrow. For close view, see figure 3.

species. Nonetheless, elms appear to be the most important hosts for *D. robusta*.

No special attempts were made to rear the maximum possible number of individuals from the slime flux cultures. It was apparent, however, that the number from any one culture was usually small (1–15 individuals), especially for samples collected in July. Most of the scrapings in which large numbers of eggs and small larvae were present were collected in June. The slime flux which produced the largest number of individuals, furthermore, was collected quite early in the spring (April 22). In this case, 141 individuals were reared from approximately 15 cc. of material scraped from a 2×2 inch area on an American Elm. These facts, together with the data from banana-trap collections, strongly imply

FIG. 3. Scar at the base of the American Elm shown in figure 2. The arrow indicates the area of slime flux from which *Drosophila robusta* was bred.

that the most extensive breeding activity by *D. robusta* occurs early in the year, resulting in an apparent population peak about the end of June.

In addition to the tabulated observations, fluxes or suspected moist areas from a number of species of trees other than those listed in table II were examined and cultured, with no success as far as *Drosophila* was concerned. These are: Catalpa, Beech, Tulip Tree, Sweet Gum, Wild Grape, Shingle Oak, Post Oak, Norway Maple, Silver Maple, Sugar Maple [2] and Box Elder.

Several exemplary individual histories of slime fluxes positive for *D. robusta* may shed some light on the problem of the suitability of breeding sites and will illustrate the variability encountered. On June 7, observations were begun on a slime flux of an American Elm situated in dense woods near Olivette, Missouri. The flux was located at the base of the trunk on an exposed root only a few inches from the ground (fig. 1). Such scars are common sites for the development of slime fluxes utilized as breeding sites by *D. robusta* (figs. 2, 3). Sap was oozing out into an oval "pocket" about a half-inch deep and measuring approximately 6 × 3 inches. The slime flux was yellowish-white, somewhat glutinous and partially covered by fallen leaves. *D. robusta* was bred from scrapings of the material taken at this time. On June 16, very large numbers of eggs and first instar larvae were found in the material, as well as older larvae. Microscopical examination of the flux at this time revealed the following main components: a matrix of bacteria in which were entangled a mass of mycelial filaments and chains of yeast cells. The latter were not abundant. The intestines of the first instar larvae contained bacteria exclusively; those of older larvae contained both yeast and bacteria. Small larvae and eggs were not obtained after June 22, indicating that the egg-laying period for this spot extended for approximately two weeks. On July 10, a number of pupae were observed, as well as third instar larvae. The pupae were congregated within one small area about an inch in diameter. Empty pupal cases and a few large larvae were observed on July 23. During this time, the macroscopic appearance of the flux was unchanged. When the tree was examined in September, sap was still emerging but no slime flux was present, and there was no evidence of the presence of *Drosophila*. It is noteworthy that although the place was examined repeatedly over a period of two months and at varying times of day, only a single adult *robusta*, a female, was seen here.

A bleeding spot was discovered on June 6 near the top of a large dry scar on a White Oak about twenty-five yards distant from the Elm described above. The moist area was about three feet from the ground (fig. 4, arrow). A distinct yeasty odor was apparent, and in contrast to the situation on the elm, a large number of adult *Drosophila* were congregated about the place. There was no slime flux of any sort present; the sap was emerging from a crevice and saturating a small area of dead wood, from which the flies were feeding. Daily visits were made to this tree from June 6 to June 25 and the flies collected in shell vials as they fed. The results were: *D. robusta*, 180 (111 ♂♂, 69 ♀♀); *D. putrida*, 17 (16 ♂♂, 1 ♀); *D. immigrans*, 14 (12 ♂♂, 2 ♀♀); *D. melanica*, 10 (5 ♂♂, 5 ♀♀); *D. nigromelanica*, 4 (1 ♂, 3 ♀♀); *D. transversa*, 2 (1 ♂, 1 ♀). Several points are of interest. The above species, with the exception of *D. immigrans*, are native ones, and *D. robusta* greatly predominates. The *affinis* group, especially *D. athabasca*, is conspicuous by its absence, since it usually predominates in banana trap collections in this woods and, in 1946 accounted for approximately 45% of all species of *Drosophila* captured there during June.

During the time that collections were being made, samples of the saturated

[2] Speiss (personal communication) has observed *D. robusta* breeding on a slime flux of this species in Braintree, Massachusetts.

wood were continually taken to the laboratory, examined and cultured. These were always negative for *Drosophila* eggs and larvae and it is clear that at this time the oak was serving as a feeding depot only. Although collections of adults were discontinued after June 25, periodic visits were made to the tree and samples of the saturated wood taken. On July 8, over a month after the spot

FIG. 4. Old scar at the base of a White Oak, at the top of which (arrow) a small patch of alcoholic flux was found. This place was used as a feeding depot by large numbers of *Drosophila* for a period of about a month. Later, slime flux developed and was utilized as a breeding site by *Drosophila robusta*. Scale is in inches.

had been originally discovered, although the macroscopic characteristics of the bleeding area were still the same, scrapings were positive for eggs and larvae of *Drosophila;* these were reared and proved to be *D. robusta.* On July 23, the bleeding spot was covered for the first time with a small mass of typical soft, brown slime flux. When visited in September, the place was entirely dry.

As a third illustrative example selected from our protocols, some of the observations made of feeding and ovipositing flies between June 17 and 22 will be given. A Slippery Elm, located on a shady but rather open lawn, was noted to have a small crack in the trunk about three feet from the ground. Sap was exuding from this place and a small amount of shallow slime flux was present. Examination revealed eggs and small larvae of *Drosophila;* these were proved subsequently to be *D. robusta.* When first discovered, about 8 A.M. on June 17, the trunk of the tree was wet all the way from the crack to the ground. At 5:30 P.M. on the same day, the entire trunk was dry, the only moisture being within the crevice itself. The place was observed intermittently during the evening, but no flies were seen. The sap suddenly began active flow about 9 P.M. The following morning, continuous observations from 5–10 A.M. were made both of this place and of a group of deliquescing fungi about 50 feet away at the base of a large Silver Maple. The two places were watched alternately for about 10 minutes' duration each.

At 5 A.M., the trunk of the tree was again wet almost to the ground; no flies were observed either on the tree or on the fungus. Except for a fairly large number of a small yellow species of *Drosophila* (probably *D. putrida*) which started feeding on the fungi about 5:30, no flies were seen at either place until 7:15, when a female *robusta* was observed alighting near the crevice on the elm. After a few exploratory feeding movements, this fly proceeded directly to the crevice and oviposited five times, with very little feeding. At 7:33 it was frightened off by a large ant. Another (or possibly the same) female alighted on the tree at 7:41 and worked deliberately toward the crevice, making exploratory feeding movements as she walked. This fly oviposited six times in the crevice until frightened by an ant at 7:56. No further *robusta* were observed on the tree up to the time that the observations were discontinued (10 A.M.). At 8:30, however, two female and one male *robusta* were noted on the fungus. All were feeding actively and continued to do so for about a half an hour, after which they performed cleaning operations, and by 10 A.M. had either flown away or were resting motionless on the bark near the base of the tree. No oviposition was noted and the behavior of the females as they fed was quite unlike that of the ovipositing females studied on the elm tree. Feeding was constant, the mouth parts being in continuous motion. Unlike the ovipositing females, the ones feeding on fungus moved very slowly and there was no such intermittent feeding or "testing" of the environment as characteristically preceded the laying of each egg on the elm.

A series of events similar to those described above was observed in the same location on several successive mornings; there was never more than a single female on the elm flux at any one time. In a number of other instances individual mature gravid female *robusta* were watched continuously as they fed on fungi. In no case was oviposition observed and in most cases the flies voluntarily flew off after making elaborate and prolonged cleaning movements.

Discussion and Conclusions

From the foregoing observations, it is clear that *Drosophila robusta* breeds abundantly on infected sap exudations of trees and that such locations represent the primary natural breeding site for this species. On the other hand, a relatively much smaller number of cases was found

of other species breeding in similar locations. As banana trap collections indicate that *athabasca* and *melanica* were abundant in the woods at the time that these studies were made, the conclusion is inescapable that these species, although they breed on slime fluxes, must also utilize some as yet undiscovered additional sites. From the extensive surveys we and others have made of fungi, it appears unlikely that this source represents the solution of the problem. The breeding sites of these species, as well as of *D. affinis,* must therefore remain in doubt.

Failure to recover *D. algonquin* at this time of year is not unexpected. Although it is abundant in banana traps in the spring, its percentage in such collections drops from 29% in May to 9% in June and to 1% in July. It is thus apparent that it breeds quite early in the year.

Drosophila victoria is an interesting case. The type of the species was described from California by Sturtevant (1942), who suggests that undescribed North American relatives of the species exist. Missouri is well out of the range of the species as described by Patterson (1943), but the species, or an undescribed one closely resembling it, has been recorded sporadically in the east. *D. victoria* is a great rarity in our banana trap collections; it has not been captured during June and July and accounts for only 0.008% of our total captures at all seasons. Except for several locations in the west, such scarcity seems to be general (Patterson 1943). Thus the implication has been that this species is rare, or at least only locally common. For this reason it was not expected in our collections from natural sources. That it was found breeding on three species of elms as well as feeding on sap from Wild Grape, Pin Oak and Cottonwood, suggests strongly that it is a slime flux breeder, although with obviously less latitude than *D. robusta.* It seems not unlikely that *D. victoria* represents an example of a species which is ordinarily not strongly attracted to baits, and may be much less of a rarity than formerly believed.

With respect to the natural breeding sites of the remaining two species listed in Group I (table I), it is clear that *D. putrida* (as well as *D. transversa* and *D. tripunctata*) is primarily a fungus breeder. *Drosophila nigromelanica,* like *D. algonquin,*[3] has yet to be recorded as breeding on native materials.

Observations of oviposition and feeding behavior, for *D. robusta* at least, suggest that an important distinction must be made between feeding and oviposition depots. Thus *robusta* has continually been observed feeding on a wide variety of deliquescing fungi with little evidence that oviposition accompanies this behavior. It is apparent, furthermore, that the reverse may also in large measure be true. That is, the evidence indicates that when a slime flux is suitable for oviposition, in many cases it attracts very few feeding flies. This tendency is illustrated in the observations on the Slippery Elm, made concurrently with those on a near-by group of fungi. In this case the latter were obviously more attractive to feeding *robusta,* flies on the slime flux on a series of successive mornings being confined to an occasional ovipositing female. We have been unable to attract *robusta,* or any members of the genus, to slime flux removed from a tree and used as bait in a cup, even though the sample was collected from a tree on which oviposition had recently occurred. A slime flux, however, undergoes obvious radical changes when deprived of its constant flow of seeping sap. Most of the slime fluxes on which oviposition was occurring, furthermore, have barely perceptible, slightly sour odors, quite unlike the yeasty fermentation odors which are generally associated with materials which readily attract feeding *Drosophila.*

In line with the above, during June

[3] This species, as well as *D. athabasca, D. robusta* and *D. putrida* were reared from a slime flux of a wild grape (*Vitis cordifolia*) in May, 1950.

the bleeding White Oak was highly attractive for *robusta* adults, although no eggs were then being laid there. Simultaneously, 25 yards away in the same woods, an American Elm slime flux was being utilized for oviposition. Despite this, on only one occasion was a single *robusta* (a female) observed there. As the White Oak became suitable for oviposition in July, furtherfore, its attractivity for the population at large seemed greatly reduced.

The implication of the above facts, for *Drosophila robusta* at least, is that ovipositing females are to some extent differentially attracted to a slime flux in a certain critical microbiological condition. On the other hand, running sap prior to the formation of slime flux, deliquescing fungi, and rotting wild or domestic fruits, appear to attract large numbers of flies of both sexes, as well as a large number of flies belonging to other species. Although no figures can be presented which show the proportion of males to females captured on slime fluxes at the critical moment when they are suitable for oviposition, what few data are available indicate a preponderance of females. On the other hand, it is interesting and possibly significant that in banana traps, and in collections of feeding but not ovipositing flies, as on the White Oak, males definitely predominate. Thus, of 5166 *robusta* collected in 1946–1948 in banana traps, 2845 or 55.1% were males. This is even more striking for certain other species, as for example *D. putrida:* of 3236 specimens trapped in 1946, 2272 or 70.2% were males. Spencer (1942) has stated that in *D. quinaria,* which shows sex ratios similar to these in banana trap collections, no such disparity exists among specimens collected directly from tomato or potato plants.

Some of the difficulties which have beset previous attempts to discover breeding sites may well have a fundamental connection with the fact, now clear for *D. robusta,* that conspicuous congregations of flies around baits or comparable natural materials do not necessarily indicate that the species is breeding there. Conversely, the evidence further indicates that a species may not necessarily congregate about its breeding sites, nor are the latter always suitable for oviposition over extended periods of time.

Such differential behavior in natural populations of *Drosophila* would carry far-reaching implications for genetic studies of population structure and variation. As more information of the type presented in this paper is accumulated, more delicate sampling methods will become possible and should result in a more precise, realistic, and ecologically sound approach to the understanding of the dynamics of intra- or inter-population genetic variability.

Acknowledgment

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Summary

1. Of 28 species of *Drosophila* found in the St. Louis (Missouri) area, about 7 may be classified as wild species common in the woods during June and July. Observations on the ecology of these species with special reference to natural breeding sites, are given.

2. *Drosophila robusta* breeds abundantly on infected sap exudations, or slime fluxes, of 13 species of deciduous trees. Of these, 9 are indigenous to the eastern United States. *D. robusta* appears to show some preference for the slime fluxes of elms and appears to breed most extensively early in the year.

3. Cases of other species of the genus breeding on slime fluxes are not numerous but the suggestion is made that *D. victoria,* and probably also *D. melanica,* regularly breed in such sites.

4. Three species (*transversa, putrida, tripunctata*) breed regularly on a wide variety of fleshy fungi.

5. *D. athabasca* has been bred sporadically from fungi, slime fluxes, and small fruits, and *D. affinis* occasionally from the

latter. Because of the obvious abundance of these species, it is clear that some additional natural breeding sites exist.

6. Individual histories of several selected breeding sites of *D. robusta* are given. The suggestion is offered that females of this species may be specifically attracted to slime fluxes which are in a condition suitable for oviposition. Large numbers of flies are rarely found about breeding sites and, conversely, congregations of this species may often be observed feeding on materials on which they are not breeding at the time. The implications of such population differentiations for future studies of the genetics of natural populations are mentioned.

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NOTES AND COMMENT

THE EFFECT OF LABORATORY CONFINEMENT ON SURVIVAL OF POISONED HOUSE MICE[1]

Laboratory findings on the toxicity of rodenticides often prove to be poor indicators of the effectiveness of the material in controlling rodent pests in the field. Low acceptability and poor accessibility of the poison as it is set out are commonly recognized factors in the wide discrepancies which may occur between toxicity findings and field performance of poisons. It is also conceivable that free-living animals in their natural habitats would react differently to ingested poisons from captive animals isolated in the customary manner in small laboratory cages during the test period.

The struggle for existence and the elimination of weak or handicapped individuals in nature have been stressed by ecologists since Darwin's time. Under such a concept, where high vitality and physical fitness are at a premium, the chances for survival of individuals incapacitated by sublethal doses of a poison would be reduced by competition with normal unpoisoned members of the population. Removal of such individuals to the artificial protection afforded by isolation in a toxicity laboratory could conceivably improve their chances for recovery. Caged wild mice, on the other hand, might suffer as a result of the physical restrictions imposed by confinement.

The experiment described in this paper was designed to compare the lethality of a standard dose of 1080 rodenticide (sodium fluoracetate) on two groups of house mice (*Mus musculus*) taken from the same habitat; one group retained in laboratory cages after treatment, the other group returned to the site of capture. Sodium fluoracetate typically produces severe convulsions within the first few hours, followed either by prompt death or by a 4- to 5-day period of debility and convalescence. During this period the animals are weak and shaky and appear to move about and feed with difficulty. It is at this time that any detrimental or beneficial effects of intra-colony association might be exerted.

In order to get a complete record of the fate of all animals after treatment, it was necessary to have access to all shelters in the habitat into which the sick animals might retreat. A colony was accordingly established in a mouse-proofed room with 500 square feet of floor space, equipped with seven large shelter boxes which could be dismantled for examination of the contents. Other studies using these shelter boxes in similar mouse-proofed rooms had proved their adequacy for populations of this general density (unpublished data). Wild house mice from nearby buildings were introduced and allowed to become established for a period of two months before the experiment was undertaken. The population density at the time of the tests, 109 active mice on 500 square feet, was close to saturation for the conditions prevailing.

The rodenticide, dissolved in water, was administered by stomach tube. Each animal was weighed and then given 13 mg. per kg. of body weight, the median lethal dose (LD50) for mice from the same population as previously determined by standard laboratory procedures.

Thirty-nine adult mice, about half of the adult population of the colony, were treated on May 13 and promptly returned to their homes where they were exposed to their untreated colony-mates for seven days. The composition of the colony at this time is shown in table I. Thirty-eight additional adults (those not treated on May 13) were taken from the colony on May 20, given equivalent doses and then placed in small cages in the manner commonly employed in laboratory toxicity tests.

TABLE I. *Size and composition of the colony at the time of the first treatment on May 13*

Adults treated and returned to the colony	39
Adults not treated	41
Total adults in the colony	80
Subadults and immatures	29
Nestlings (in nests)	29
Total population	138

All animals were checked periodically and

TABLE II. *Mortality and condition of survivors at intervals after administration of the poison. Group A—mice that were returned to the colony. Group B—mice that were held in laboratory cages*

Time after dosing (hours)	Group A (colony)			Group B (cages)		
	Dead	Sluggish	Active	Dead	Sluggish	Active
0	0	0	39	0	0	38
2	0	39	0	11	27	0
9	9	30	0	12	26	0
24	18	21	0	20	18	0
48	21	2	16	22	?	?
100	22	0	17	22	0	16

[1] This work was supported in part by a grant from the Public Health Service, National Institutes of Health.

counts made of dead, clearly sick and apparently well animals. The data are presented in table II. The onset of mortality was slower in the released mice than in those retained. The reasons for this are not known. At the end of 9 hours mortality was only slightly greater in the laboratory group than in the colony group. At 25 hours the two were nearly even, and at 100 hours, when all survivors had largely or completely recovered, the number dead was 22 in each, 56% of the total in the released group, 58% in the confined group. There was thus essentially no difference in the reaction of the two groups to the LD50 dose.

These results suggest that the standard laboratory tests of toxicity of 1080 rodenticide are reasonably indicative of its lethality in actual suppression programs under field conditions.

Summary

A group of wild house mice (*Mus musculus*) from a large enclosure with cover facilities simulating natural conditions for the species was given median lethal doses of 1080 rodenticide and then returned to their familiar surroundings and colony associates. Another group from the same enclosure was given the same treatment and then held in small laboratory cages in the manner customarily used in standard laboratory toxicity tests. Survival in the two groups was essentially the same.

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A METHOD FOR INVESTIGATING THE RELATIONSHIP BETWEEN THE DISTRIBUTION OF INDIVIDUALS OF DIFFERENT SPECIES IN A PLANT COMMUNITY

One of the most important trends in current ecological research is the analysis of the patchiness that exists within all plant communities; a patchiness that may have its basis in the preference of particular species for particular habitat conditions which vary in different parts of the community (Jowett and Scurfield 1949), these habitat conditions being in some cases determined by the pre-existing plants—a situation often resulting in cyclical successions taking place on unit areas of the community (Watt 1947)—or in the aggregation of individuals of the same species dependent upon their means of reproduction and spread (*e.g.*, Clapham 1936). Other bases of patchiness within a plant community may well be demonstrated by future research but so far it is clear that the concept of a plant community as consisting of randomly distributed individuals has been completely overthrown. This, however, does not imply a return to the concept of a plant community as having a closely integrated structure analagous to that of a living organism. Patchiness can exist without structure for the latter term can only justifiably be used when the spatial relationships of the constituent plants are determined by the interactions of the existing plants themselves, one on another. The term "patchiness," however, implies a spatial correlation between individuals of a species with individuals of the same or of a different species, irrespective of the basis of this correlation. It is the aim of this paper to briefly indicate the value of what may be termed interspecific correlation coefficients in revealing certain types of patchiness.

An interspecific correlation coefficient may be said to be an estimate of the tendency of individuals of one species to be present in the neighborhood of individuals of a second species. To take a definite example. Steiger (1930) scored, among other things the number of individual plants of *Andropogon furcatus, A. scoparius, Bouteloua curtipendula* and *Poa pratensis* in each of 40 quadrats used in sampling High Prairie Grassland. His published data give the number of individuals of each of these species that was found in each of the 40 quadrats. From these data we can calculate the partial correlation coefficients between the number of individuals of *A. furcatus* and *A. scoparius,* between *A. furcatus* and *B. curtipendula* and so on. The values of these coefficients are set out in table I.

These values indicate that those quadrats that contain a large number of individuals of *A. furcatus* tend to contain a large number of individuals of *P. pratensis,* while those quadrats that contain a large number of individuals of *A. scoparius* tend to contain a large number of individuals of *B. curtipendula.* The significance of these correlations is enhanced when we find

Table I. *Interspecific correlation coefficients between the four most abundant species in High Prairie Grassland calculated from data obtained by Steiger (1930)*

Species	Partial correlation coefficient	P
A. furcatus, P. pratensis	+0.38	0.02
A. furcatus, B. curtipendula	+0.25	$\gg 0.1$
A. furcatus, A. scoparius	−0.28	0.09
P. pratensis, A. scoparius	−0.08	$\gg 0.1$
P. pratensis, B. curtipendula	+0.09	$\gg 0.1$
A. scoparius, B. curtipendula	+0.53	$\ll 0.01$

TABLE II. *As table I but for low prairie grassland*

Species	Partial correlation coefficient	P
A. furcatus, P. pratensis	+0.51	≪0.01
A. furcatus, B. curtipendula	−0.01	≫0.1
A. furcatus, A. scoparius	−0.29	0.07
P. pratensis, A. scoparius	+0.05	≫0.1
P. pratensis, B. curtipendula	+0.08	≫0.1
A. scoparius, B. curtipendula	+0.44	≪0.01

essentially the same correlations on analyzing the analagous data that he gives for 40 quadrats of Low Prairie Grassland. These values are set out in table II.

As far as I know the only previous record of the calculation of an interspecific correlation coefficient from quadrat data occurs in Hanson's paper on the Native Prairie in Western North Dakota (Hanson 1934). He calculated the correlation coefficient between the number of stalks of *Agropyron smithii* and the area covered by *Bouteloua gracilis* and found that it was −0.09 which was not significantly different from 0.

Having demonstrated that this method of analyzing quadrat data may yield interesting results we now pass to consider the general ecological interpretation of interspecific correlation coefficients. Strictly a positive coefficient between species A and B only tells us that those unit areas of the community that contain a large number of individuals of species A tend to contain a large number of individuals of species B, and a negative coefficient that those unit areas of the community that contain a large number of individuals of species A tend to contain a small number of individuals of species B. A further interpretation in ecological terms cannot be deduced from the quadrat data but only by a further examination of the community. The possible ecological interpretations fall into two groups.

a) The presence of individuals of species A modifies the neighboring environment in such a way as to make it either more or less favorable to individuals of species B.

b) A particular biotic or physical factor or a combination of such factors varies in different parts of the community and this variation either affects the distribution of individuals of species A and B similarly (giving a positive correlation between A and B) or in opposite directions (giving a negative correlation between A and B).

The ecological significance of interspecific correlation coefficients is, however, somewhat complicated by the fact that an individual plant occupies a finite area. This means that there can only be a finite number of individual plants in any single quadrat. This spatial exclusion can result in both positive and negative correlation coefficients that have no ecological significance. Let us consider a hypothetical case in which 50 per cent of the quadrats each contain about 10 individuals of species A and about 10 individuals of species B but no individuals of species C, while each of the remaining quadrats contains one individual of species C and this individual occupies half the area of the quadrat thus leaving room for only about 5 individuals of each of the species A and B. If data were collected only on species A and C or only on species B and C negative correlation coefficients would be found. If only on A and B the correlation would be positive. If, however, we have data for all 3 species the calculation of partial correlation coefficients would eliminate this exclusion effect. It would thus appear that if data on all the more abundant species are available the calculation of partial correlation coefficients will eliminate any effects of spatial exclusion. This deduction, however, implies that the number of individuals of any one species in a quadrat is a measure of the exclusion effect of that species in that particular quadrat. If the individuals of a particular species vary greatly in size there may be an almost total absence of any correlation between the number of individuals of that species in each quadrat and the area these individuals occupy. Taking this into account it would be more accurate to say that the calculation of partial correlation coefficients *tends* to take account of the exclusion of one species by another. The effects of spatial exclusion will be further reduced by using quadrats that are large relative to the areas occupied by the individual plants.

It is also worth while noting that should the density of individual plants of all species be greater in one part of the community than another a positive correlation would be found between any 2 species. By collecting data on more than 2 species and calculating partial correlation coefficients this variation also would tend to be eliminated.

If data are available on four species (A, B, C and D) and the interspecific correlation coefficient (partial or otherwise) between A and B is negative and that between C and D is negative and there are no significant negative or positive correlations between A or B and C or D, the correlations must have ecological significance. Similarly if two independent positive coefficients are found, as in the analysis of Steiger's data above, or independent negative and positive correlations, they also must have ecological significance.

This paper has sought to demonstrate the value and the limitations of interspecific correlation coefficients as a tool in the analysis of quadrat data. It is suggested that useful clues to the spatial arrangement of plants of different species in a community might be obtained by such an analysis thus crystallizing problems for

investigation in the field. It is often possible to tell by inspecting a correlation table (*i.e.*, a table which has as its axes, number of individuals of species A and number of individuals of species B, and in which each quadrat is recorded) whether it is likely to be profitable to grind out the correlation coefficients. A convenient account of the method of calculating such coefficients will be found in Fisher (1946). Even inspection of data that simply shows the presence or absence of the different species in each quadrat may prove useful.

Summary

1. The possibility of demonstrating spatial correlations between individuals of different species in a plant community by calculating interspecific correlation coefficients from quadrat data is shown in an analysis of Steiger's data on prairie grasslands.

2. The interpretation of interspecific correlation coefficients is briefly discussed.

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OUTLINE FOR ECOLOGICAL LIFE HISTORY STUDIES IN TREES, SHRUBS, AND STEM SUCCULENTS[1]

Introduction

The present paper is another in the series of outlines and bibliographies of ecological life history studies of both plants and animals which are currently appearing in Ecology, under the sponsorship of the Committee on Ecological Life Histories. The following outline and literature review concerns plants belonging to the *phanerophyte* life form as defined by Raunkiaer (1934). These are plants whose perennating or renewal buds are located appreciably above the ground where they are exposed to the atmosphere during the unfavorable season (which may be either cold or dry). The group includes all deciduous and evergreen trees, shrubs, woody lianas, stem succulents, tropical tree-herbs, epiphytes, and many parasites, belonging to several major plant groups. The following discussion and bibliography, however, include only angiosperm and gymnosperm phanerophytes which are either woody or succulent.

The objectives of autecological research may be varied. Much stimulus has come from the economic importance of certain species, and a great deal of pertinent autecological information has been gathered in the process of attempting to solve practical problems. On the more theoretical side, ecological life histories have much to contribute to an understanding of the distribution of species, as well as aiding in the solution of such general biological problems as environmental response, adaptation, and speciation. Another theoretical objective of life history studies is that of helping to explain the structure and dynamics of communities themselves, since only from the working out of the complexities of the ecology of the important species of a community can a sound basis be provided for an understanding of vegetational problems. Furthermore, the value of ecological life history work in teaching has not yet been fully recognized. A laboratory outline for the study of the American elm has been successfully used for several years in advanced classes in Experimental Ecology by Dr. D. B. Lawrence (1947) at the University of Minnesota.

It will be readily apparent from the following outline that the solving of most of the ecological problems concerning even a single species would require much more time and effort than is ordinarily available to one person. Consequently most autecological data accumulate over ex-

[1] The writer is indebted to Dr. D. B. Lawrence of the University of Minnesota for help in compiling the bibliography, criticism of the manuscript, and for other aid. Much material for the outline and bibliography was obtained from the Experimental Ecology Laboratory Guide (Lawrence 1947).

tended periods of time from numerous studies which are of a local or limited nature and of short duration, rather than from the more desirable detailed and comprehensive long term studies. There is a need, however, for survey studies which integrate the known ecological data concerning a given species, clarify the important problems, and attempt to fill in some of the wider gaps in our knowledge of the species. In Britain this need is partly being filled at the present time by the accounts being published in the "Biological Flora of the British Isles," currently appearing in the JOURNAL OF ECOLOGY. This series was first proposed by E. J. Salisbury (1928), but was not actually begun until thirteen years later (Anonymous 1941). A revised outline for contributors has since been published (Anonymous 1947). Possibly it would not be premature to consider initiating a "Biological Flora of North America" within the near future.

METHODS

Much can be learned about the environmental relations of a species from critical observation alone. Indeed, the more important and fruitful lines of research can often be suggested and guided by field observations, thus saving much waste from undirected effort. It is essential, however, that hypotheses concerning the ecology of a species be substantiated by quantitative data, and experimental work is particularly desirable. The broad range of topics to be investigated in the attempt to make a relatively complete ecological life history survey require the use of a wide variety of techniques, but elaborate equipment is not usually necessary. Among the various types of methods which may be necessary are techniques of sampling communities, transplant and greenhouse studies, field experimentation, habitat analysis, measurements of growth, laboratory experimentation, and even histological methods. Consequently, no attempt will be made here to cover with any completeness the literature which describes possibly useful techniques. A number of references describing methods of rather general application will be mentioned, however. An extensive literature has developed around environmental analysis. An excellent review of methods of soil analysis is presented from an ecological point of view by Lutz and Chandler (1946). Methods of measuring light are discussed by Shirley (1945), and day-length in particular by Post (1942). Measurement of other climatic and some biotic factors, in addition to soil and light, are discussed by Bates and Zon (1922), Daubenmire (1947), and Gates (1949). General exclosure techniques for studying the effects of animals on plants are evaluated by Daubenmire (1940).

A discussion of the local population (biotype or biotypes) as the basic unit of autecological research is presented by Lawrence (1950). Here also is emphasized the caution that is necessary in taking material on ecological behavior from the literature which applies to one local population and applying it to the study of another local population of the same taxonomic species growing in some other part of its natural range. Camp (1942) has pointed out the problems involved in studying the ecology of species reproducing by apomictic seeds. Methods and interpretations of transplant experiments in studying the variability of species are reviewed by Hiesey (1940). Procedures for ascertaining the community affinities, frequency, and dominance of species are described by Braun-Blanquet (1932), and methods of mapping and sampling of vegetation are outlined by McLean and Cook (1946), and Gates (1949). Instruments for studying rate of diameter growth of woody plants are described by MacDougal (1938) and Daubenmire (1945). Sampling and interpreting stem growth layers are discussed by Glock (1937). Problems involved in phenological observations are evaluated by Leopold and Jones (1947). Methods of studying root characteristics are presented by Weaver (1919), Sayre and Morris (1940), and Tharp and Muller (1940).

The techniques of ascertaining the day-length requirements of plants are given by Allard and Garner (1940). Methods of observing insect pollinators and the anthokinetic cycle are described by Clements and Long (1923). Brink (1924) and Righter (1939) discuss the techniques and problems involved in determinations of pollen viability. Techniques for carrying on controlled pollination and pedigreed seed production in phanerophytes, particularly species of pines, are described by Cumming and Righter (1948). Methods of collecting, handling, and testing of fruits and seeds are presented by the Association of Official Seed Analysts of North America (1938), Baldwin (1942), and the Forest Service (1948). Precautions which should be taken in seed germination tests of native plants are outlined by Lawrence, Lawrence, and Seim (1947). Two potentially useful methods of testing viability of dormant seeds are evaluated by Flemion (1948), and Flemion and Poole (1948). Much additional information in seed technology is reviewed by Porter (1949). Useful techniques for studying the effects of bird or mammal ingestion upon seed dormancy and viability were used by Krefting and Roe (1949). The value of exclosures in studying rodent damage to soil-stored seeds is described by Moore (1942). Methods of estimating and interpreting the reproductive capacity of plants are discussed by Salisbury (1942).

GENERAL REFERENCES

When beginning a detailed investigation of one or a few species, or when merely attempting

to become acquainted with the ecology of the commoner species in a region with which one is not familiar, there are usually a number of useful references which may be consulted. There are first of all many manuals and annotated species lists, which, although primarily taxonomic, frequently contain valuable ecological notes concerning the distribution, habitats, abundance, flowering period, performance, longevity, and fruit and seed structure of individual species. Examples of outstanding publications of this type are those of Sudworth (1908, 1915, 1916, 1917, and 1934) covering the trees of the western United States; of Sargent (1891–1902), and Preston (1948) which include the trees of North America; and a number of publications covering state-wide or somewhat larger areas, such as that of Jepson (1910) on the trees of California, of Miller and Tehon (1929) on the trees of Illinois, of Benson and Darrow (1945) on the southwestern desert trees and shrubs, and of Benson (1950) on the cacti of Arizona. Manuals or annotated species lists of a much more local scope also frequently contain considerable autecological information. Both regional and local publications with a taxonomic emphasis are listed geographically by Blake and Atwood (1942).

Other sources of ecological data are some of the taxonomic monographs of genera. For detailed studies such monographs are also extremely valuable in clarifying the problems of nomenclature and species status which are prerequisite to autecological studies. A number of general reviews are also available covering the autecology of many economically important trees, such as those of Betts (1945), Cheyney (1942), and Green (1938). Another valuable source of autecological information are the many detailed vegetational studies which are scattered throughout the periodical literature. The literature of economic entomology, and wildlife management, and of forestry, range management, horticulture, plant pathology, plant breeding, and other applied plant sciences is similarly rich in information concerning many trees and shrubs of relatively little, as well as those of great, economic importance.

There are a number of references which catalogue species according to particular points of view. For nomenclature, Little (1944), and Kelsey and Dayton (1942) are useful. Fossil records of genera and species are recorded by Knowlton (1919), and chromosome counts by Darlington and Ammal (1945). Wildlife usage as well as some other valuable information is recorded by Van Dersal (1938), and Dayton (1931) discusses the browse-value of trees and shrubs. The more valuable honey plants are listed by Pellett (1923). Wild medicinal plants are considered by Henkel (1906), and Yanovsky (1936) lists the food plants of the North American Indians. Medsger (1939) and Fernald and Kinsey (1943) have cataloged the edible wild plants of eastern North America.

The more common diseases of trees are discussed from an ecological point of view by Baxter (1943), and Graham (1939) similarly covers forest insects. A more comprehensive catalogue of forest insects is given by Doane *et al.* (1936), and a host index of North American fungi has been compiled by Seymour (1929). The known occurrence of mycotrophy is reviewed by Kelley (1950). A bibliography on roots of forest trees has been prepared by Dunning (1949).

Insect pollinators of a large number of plant species are catalogued by Knuth (1906–09), and Robertson (1928). Pollen longevity of many phanerophytes and other plants is recorded by Holman and Brubaker (1926). Embryo development is extensively treated by Johansen (1950). Seed and seedling characteristics of the woody plants of the United States are discussed by the Forest Service (1948), and for some species of other regions by Lubbock (1896). The distribution of self-sterility is reviewed by East (1940), and of apomixis by Stebbins (1941). Dispersal mechanisms of plants are catalogued by Ridley (1930). Information on the longevity of plants has been compiled in the volume by Molisch and Fulling (1938). A bibliography of considerable ecological value is that of Munns (1940) covering North American forestry.

Representative Studies

As might be expected, the phanerophytes which have been studied most thoroughly from an ecological point of view have been those of greatest economic importance, yet others of similar importance have been unaccountably neglected. Silviculturists appear to have been among the first to recognize the value of balanced reviews of the present status of knowledge concerning particular tree species. Consequently, a large proportion of the studies cited in the bibliography are of this type, usually, but not always, strongly emphasizing the economic problems involved. Among the more thorough and balanced of these publications are those of Spaulding and Fernow (1899) on *Pinus strobus* (white pine); of Ashe (1915) on *Pinus taeda* (loblolly pine); of Mattoon (1915a) on *Taxodium distichum* (southern cypress); of Murphy (1917) on *Picea rubens* (red spruce); of Troup (1921) on *Shorea robusta* (Sāl); of Korstian and Brush (1931) on *Chamaecyparis thyoides* (southern white cedar); and the relatively recent monograph on *Pinus palustris* (longleaf pine) by Wahlenberg (1946).

Several works by silviculturists which are very detailed but limited to problems involved in the natural reproduction of certain tree spe-

cies are those of Pearson (1923) on *Pinus ponderosa* (western yellow pine); of Korstian (1927) on *Quercus* species; of Haig *et al.* (1941) on *Pinus monticola* (western white pine); and of Isaac (1943, 1949) on *Pseudotsuga taxifolia* (Douglas-fir).

The survey studies of phanerophytes by ecologists have generally been more limited in time and space than those of silviculturists, who have been able to benefit from the coordinated research of many individuals. The Biological Flora of the British Isles has included accounts of about five trees and shrubs (Godwin 1943, Jones 1945, Chapman 1947). Examples of brief survey types of studies are those of Phillips (1909) on *Pinus edulis* (piñon pine), and of Chu and Cooper (1950) on *Metasequoia glyptostroboides* (dawn-redwood). Other type studies, usually emphasizing particular ecological aspects, are those of Shreve (1910, 1911) on *Cereus giganteus* (giant cactus) and on *Parkinsonia microphylla* (palo verde), respectively; Cooper (1917, 1922) on *Sequoia sempervirens* (redwood), and *Ribes* species, respectively; Humphrey (1937) on *Aplopappus fruticosus* (burroweed); Turner and Costello (1942) on *Opuntia polyacantha* (prickly pear); and Sealy (1949) on *Arbutus unedo* (strawberry-tree). A more detailed type of monograph is that of Davis (1940) on *Rhizophora mangle* (mangrove) in Florida. Many more ecological surveys of particular species are listed in the bibliography. Specialized autecological studies of limited scope are more frequently made than is the survey type of investigation, but these are not included in the literature references which follow. An exhaustive search of the literature was not attempted, and the writer would welcome having omissions brought to his attention. Only works in the English language are included.

Suggested Outline

Taxonomy: Definition and description of the species (or other unit) under study, and its genetic uniformity.

Nomenclature.—Valid scientific name; frequently used synonyms; common names, their origin, and regions where they are used; names of subgenus, section, and family.

Distinguishing features.—Life form; taxonomic description of the species and of recognized subspecific units; field recognition features of both growing and dormant aspects of seed, seedling, juvenile, mature, and senescent stages.

Variability.—Number of recognized subspecific units (such as subspecies, varieties, forms, ecotypes, pure lines, strains, and clones); definitions of the local populations or units studied in terms of their genetic variability and distribution; available knowledge concerning genetics, speciation, and chromosome number; occurrence of natural or artificial hybrids; somatic plasticity.

Importance: Ecological and economic significance of the species (considering the effects of genetic variability).

Ecological significance.—Degrees of dominance and subordination exhibited in various vegetation types and regions; role in succession; relation to animals.

Economic relations.—Weedy or poisonous characteristics; value for browse, timber, pulp, honey, fruits, watersheds, wildlife, windbreaks, erosion control, ornament, and other purposes; use by aborigines and early settlers.

Occurrence: Regions and habitats in which the species occurs, with its distribution and abundance in each in both the past and in the present (considering the effects of genetic variability).

Range.—Distribution and abundance by regions, including: Known geographical range limits; altitudinal limits; relative abundance in different regions and altitudes; fossil records, and hypotheses of place and time of species origin, past distribution, and migration routes.

Habitats—general statements.—Distribution and abundance by habitats, including: Classification and introductory description of habitats where the species occurs; average and extreme types of habitats; variations of most frequently occupied habitats in different regions.

Climate.—Average and extreme climatic conditions where the species occurs, including: Climatic classifications; monthly or seasonal temperatures and precipitation; cloudiness and humidity; length of growing season; photoperiods; frequency and severity of extremes (such as drought, flood, frost, intense cold, hail, glaze, wind, and others); light intensity; microclimatic limitations.

Physiography.—Average and extreme topography and other physiographic conditions where the species occurs, including: Angle and direction of slope; association with certain topographic features (such as swales, ravines, streamsides, swamps, hilltops, bluffs, or cliffs); correlation of topographic location with other environmental factors (such as with exposure to frost or to dry or cold winds; with the angle of the sun's incident rays in various seasons and the amount of shading; with the accumulation of drifting snow, or runoff from precipitation; with accessibility to livestock, lumbering operations, or other influences; or with the occurrence of favorable or excluding types of vegetation); occurrence of landslides, mudflows, wind burial or excavation, and water erosion.

Soil.—Average and extreme conditions of the soil or other substrata where the species occurs, including: Nomenclature of soil series and types; the soil profile; the water table and its fluctuations; the geologic substratum and parent

material; the characteristics of each major horizon regarding depth, permeability, organic content (including type and depth of surface litter), texture, colloid content, stoniness, exchangeable calcium, free carbonates, pH, nutrient elements, aeration, toxic substances, salinity and erodibility.

Fire.—Average and extreme occurrence of fire where the species occurs, including: Frequency and severity of fires in the past and in the present; relation of fire to region, climate, physiography, vegetation type, and human influences; causes of fire.

Communities.—Average and extreme biotic communities in which the species occurs, including: Vegetation types and community characteristics; frequency and distribution of the species in each; its gregariousness and degree of dispersion; its most constantly associated species; occurrence of mycorrhizal and symbiotic nitrogen-fixing fungi and bacteria, injurious organisms and competitors, and organisms beneficial in pollination, dispersal, and other processes.

GROWTH: Characteristics of the vegetative or non-reproductive organs and their response to habitat differences (considering the effects of genetic variability).

Shoot growth.—Growth habits of shoots, including: Comparative responses in different habitats; effects of plant age and vigor; phenology; periodic growth cycles; colony characteristics if clones tend to form clumps; stem height, diameter, weight, and branching; total lengths and weights of twigs produced annually or per unit time; shoot bud, bark and growth layer characteristics; leaf number, size, shape, area, color, and weight; relevant physiological data (such as transpiration surfaces and rates, photosynthetic efficiency, osmotic values, food storage in the shoot, relative mineral element requirements, and ash content of leaves and wood); specific temperature, light, and other environmental requirements for shoot growth; methods of inducing satisfactory shoot growth in cultivated plants.

Root development.—Growth habits of roots, including: Comparative responses in different habitats; effects of plant age and vigor; phenology; general classification of root system; root depth, spread, diameter, weight, and branching; bark and growth layer characteristics; total lengths and weights of roots produced annually or per unit time; root-shoot ratios; occurrence of natural root grafts; occurrence, necessity, and morphological effects of mycorrhizal and symbiotic nitrogen-fixing fungi; relevant physiological data (such as surface of absorbing tissues, ability to accumulate deficient elements, food storage in the roots, and internal conditions influencing root-shoot ratios); specific temperature, moisture, oxygen, and other environmental requirements for root growth; methods of inducing satisfactory root development in cultivated plants.

Resistance.—Response and resistance of non-reproductive organs to physical and biotic extremes, including: Comparative responses in different habitats; effects of plant age and vigor; response and resistance to physical extremes of drought, flood, frost, intense cold, hail, glaze, snow, wind, short or cool growing seasons, soil burial or erosion, water table fluctuations, shallow soils, impermeable horizons, poor soil aeration, extremes of pH, salinity, toxic substances, nutrient deficiencies, and frequent or severe fires; response and resistance to injurious biotic factors such as plant competition, parasitic fungi, injurious insects and other invertebrates, rodents, birds, the large herbivores, and other indigenous vertebrates (including the ecology of the injurious organism); resistance to human activities, such as injury by domesticated animals, felling or cutting, soil tillage, grubbing, and tapping or wounding; methods of controlling or eradicating species where it is a weed; methods of protecting cultivated plants against physical and biotic extremes; evaluation of the physical and biotic extremes affecting vegetative growth in terms of their relative importance for species survival.

Longevity.—Lengths of life of leaf, stem, and root, including: Comparative responses in different habitats; effects of plant vigor; average and maximum longevity; changes in growth and reproductive activity associated with senescence; natural occurrence and causes of rejuvenation; evaluation of the causes of death; methods of rejuvenation or prolonging life in cultivated plants.

REPRODUCTION: Characteristics of sexual and asexual reproductive organs and their responses to habitat differences (considering the effects of genetic variability).

Initiation.—Initiation and development of flower buds (or cones), including: Comparative responses in different habitats; effects of plant age and vigor; gross morphological development; phenology; quantity of flower bud (or cone) production; specific temperature, photoperiod, and other environmental requirements for initiation and development of flower buds (or cones); physical and biotic factors injurious to flower buds (or cones), and their evaluation; methods of inducing satisfactory bud (or cone) development in cultivated plants.

Pollination.—Flowers (or pollinating cones), and the processes of anthesis, pollination, and fertilization, including: Comparative responses in different habitats; effects of plant age and vigor; gross morphology of flowers (or cones) and pollen; phenology and the anthokinetic cycle; physical agents of pollination and conditions influencing their effectiveness; biotic agents

of pollination, their relative effectiveness, and their ecology; effective range of pollen transport; flower and pollen characteristics shown to be functional in attracting pollinators or in favoring cross- or self-pollination; pollen quantity, viability, longevity, and germination requirements; occurrence of cleistogamy, parthenocarpy, and apomixis; specific temperature, photoperiod, and other environmental requirements for anthesis, pollination and fertilization; physical and biotic factors injurious to flowers (or cones), to pollen, or to the pollinating organisms, and their evaluation; methods of collecting and storing pollen, or of inducing satisfactory flowering, pollination, and fertilization in cultivated plants.

Maturation.—Maturation of fruits (or cones) and seeds, and their natural storage before dispersal, including: Comparative responses in different habitats; effects of plant age and vigor; gross morphology of maturing fruits (or cones) and seeds; phenology; proportion of fruits (or cones) set and matured based on buds and flowers produced; season, severity, and causes of premature abscission; occurrence and causes of periodic bearing; quantity of fruit (or cone) production; differences between early and late matured fruits (or cones) and seeds; seed viability; occurrence and effects of natural storage of mature fruits (or cones) on the plant before dispersal; relevant physiological data (such as favorable carbohydrate-nitrogen ratios or other internal requirements for setting and maturing of fruits (or cones) and seeds; food storage in the seed); specific temperature, photoperiod, and other environmental requirements for maturation; physical and biotic factors injurious to fruits (or cones) and seeds before dispersal, and their evaluation; methods of controlling fruit (or cone) production in cultivated plants.

Dispersal.—The structures and agents involved in dispersal, including: Comparative responses in different habitats; gross morphology of fruits (or cones) and seeds at the time of dispersal; physical agents of dispersal and conditions influencing their effectiveness; biotic agents of dispersal, their relative effectiveness, and their ecology; fruit (or cone) and seed characteristics shown to be conducive to specific types of dispersal; season of dispersal; dispersal distances; physical and biotic factors injurious to fruits (or cones) and seeds during dispersal, or to the dispersal organisms, and their evaluation.

Dormancy.—Storage of seeds following dispersal but preceding germination, including: Comparative responses in different habitats; location of natural storage following dispersal; morphological changes occurring to fruits (or cones) and to seeds while in natural storage; intensity and variation of inherent seed dormancy; specific temperature, moisture, and other environmental requirements for maintaining or breaking of seed dormancy in nature; longevity of seeds in nature; relevant physiological data (such as the physiological causes of seed dormancy); physical and biotic factors injurious to dormant seeds following dispersal, and their evaluation; methods of collecting, extracting, cleaning, storing, and breaking of dormancy of seeds of cultivated plants.

Germination.—The process of seed germination, including: Comparative responses in different habitats; gross morphology of germination; phenology; location of germination in nature; specific temperature, moisture, light, pH, aeration, and other environmental requirements for germination; physical and biotic factors injurious to germinating seeds, and their evaluation; methods of obtaining satisfactory germination in cultivated plants.

Establishment.—Growth and establishment of the seedling, including: Comparative responses in different habitats; gross morphology of developing seedling; phenology; location and abundance of seedlings in nature; rapidity of root growth in depth, spread, and branching; seeding root-shoot ratios; time of exhaustion of stored foods; age of infection with mycorrhizal or symbiotic nitrogen-fixing fungi or bacteria, and their effects upon the seedling; differences attributable to nongenetic variations in amount of food stored in the seed; specific temperature, moisture, light, and other environmental requirements for seedling establishment; periodicity of seedling establishment, its relation to climate and other environmental conditions, and to periodic seed production; physical and biotic factors injurious to seedlings, and their evaluation; time-frequency curves of seedling survival; evaluation of the stages in the seed reproductive cycle in terms of mortality and species survival; methods of inducing satisfactory seedling growth and establishment in cultivated plants.

Asexual reproduction.—Structures and processes involved in asexual reproduction, including: Comparative responses in different habitats; effects of plant age and vigor; gross morphology of organs functional in asexual reproduction; phenology; production, growth habits, and longevity of asexual reproductive structures, and characteristics of the resulting plants; rates of reproduction by asexual means; comparison of sexual and asexual reproduction in terms of their relative effectiveness; relevant physiological data (such as the physiological balance between sexual and asexual reproduction; food storage in asexual reproductive organs); specific environmental requirements for asexual reproduction; physical and biotic factors injurious to organs of asexual reproduction, or to the resulting developing plants, and their evaluation; evaluation of the stages in the

asexual reproductive cycle in terms of mortality and species survival; methods of vegetative propagation in cultivated plants.

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THE MISUSE OF CLIMATE AS AN INDICATOR OF VEGETATION AND SOILS

The early American ecologists and Russian pedologists popularised the idea that climate is the controlling factor in the formation of vegetation and of soils. They developed the climatic classification of vegetation and the zonal classification of soils. It is true that in certain restricted areas classificatory schemes based on climatic control are applicable, but the general statement that climate can be used as an indicator of either vegetation or of soil is frequently incorrect.

During the past few years pedologists have come to realize that climate is not always the dominant factor in soil formation. The outstanding contribution to soil science by Jenny (1941) leaves little doubt as to the inap-

plicability of climatic classification to the North American Continent, while the recent paper by Hallsworth and Costin (1950) fully substantiates Jenny's arguments and their applicability to the Australian Continent.

Unfortunately, plant ecologists and geographers dealing with vegetation and soils maps are still dominated by the monoclimax theory. Consequently vegetation and soils maps of continents constructed from climatic data on the supposition that climate is the controlling factor are continually being produced. At the same time these maps are used to illustrate the close correlation between climate, vegetation and soils! I refer in particular to the article by Blumenstock and Thornthwaite (1941) in which are included vegetation and soils maps of the continent of Australia. The boundaries in these maps have been fixed on the assumption that the climate-soils-vegetation correlations for the North American Continent apply to the Australian Continent. This is far from true.

To quote a specific example: The climate of the State of New South Wales in south eastern Australia is classified climatically by Blumenstock and Thornthwaite into four major zones, Humid, Sub-humid, Semi-arid and Arid. No Australian would contend this statement. The vegetation of New South Wales is classified as forest, steppe and desert. The steppe vegetation (steppe being defined as "a term at once descriptive of a semi-arid climate and a short grass vegetation") supposedly occupies some 60 to 70 percent of the State and the vegetation boundaries delineated on the map show a remarkable correlation with the climatic boundaries. But in reality the so-called steppe vegetation of New South Wales (Beadle 1948, and unpublished data) consists not of short grass, but of woodlands of *Eucalyptus* some 20 to 50 feet in height, scrubs of *Acacia* and *Casuarina* 15 to 20 feet in height, and mallee scrubs of *Eucalyptus* 15 to 20 feet in height. A few small areas of grassland analogous to the North American tall grass prairies do exist, as well as larger areas of saltbush, analogous to the sagebrush country of North America.

It is unwise to apply climate-vegetation correlations or climate-soil correlations deduced in one continent for the construction of either vegetation or soil maps of another continent for the following reasons:—

In climatically similar areas on two different continents (and even on the same continent) the other factors affecting vegetation and soils are not necessarily the same, or even similar. In fact, the chances are that they will be dissimilar, firstly in the species available to the areas and in the various degrees of adaptation of these species, and secondly in the parent materials of the soils, which affect both soil and vegetation.

Differences in the available species naturally lead to floristic differences in the plant community. Structural differences likewise occur because certain species or groups of species have become singularly adapted to a limiting climatic factor—low rainfall in Australia, low temperatures in North America. Thus in Australia certain species of *Eucalyptus, Acacia* and *Casuarina* (and others less abundant), have become so efficiently adapted to semi-arid and arid conditions that they form tall woodlands and scrubs in climates which in North America support grassland. That some of the Californian grasslands have remained as grassland because of the lack of highly adapted woody species is well illustrated by the present natural migration of recently introduced Australian eucalypts into California; thus the grassland of the Berkeley (California) district is steadily being converted into a forest. If *Eucalyptus* had reached North America naturally, or had evolved there, then the climate-vegetation correlations of the two continents would have been similar.

Again the tree line (*Eucalyptus* spp.) in Australia stands at about 6,000 feet on the mainland and 4,000 feet in Tasmania. Consequently if an Australian ecologist were to construct a vegetation map of North America on the assumption that climate is a reliable indicator of vegetation, he would place the tree line in America at some 6,000 feet. But species of *Picea,* which have become better adapted to the cold than any species of *Eucalyptus,* form tall forests in America at altitudes of 9,000 or 10,000 feet, in latitudes comparable to the Australian alpine (treeless) areas.

Just as the available species can upset climate-vegetation correlations, so also can a soil property. For example the natural grassland areas of New South Wales and the saltbush communities occur on patches of heavy textured soils among otherwise continuous areas of forest, woodland, or scrub growing on light textured soils. Again, the deficiency of a soil nutrient commonly leads to the development in Australia of a low heath in country which, climatically, would be expected to produce woodland or forest.

What has been said about vegetation applies likewise to soil. The podsol strip, so faithfully reproduced from map to map along the southeast coast of Australia, is a mosaic of the following soil groups at least: podsols, grey and brown podsolic soils, red loams (laterites of the American workers), rendzinas, brown forest soils, prairie soils and lithosols. Similarly the other so-called soil zones of Australia are mosaics.

Since simple correlations established in small

areas are of little or no value for general use, it follows that vegetation and soil maps can be constructed only by direct observation. There are no short cuts—unless one knows all the independent variables.

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ADDITIONAL NOTE ON THE INTERRELATIONS OF PHYTOSOCIOLOGICAL CHARACTERS

It has been called to our attention that an ambiguous statement in our recent article (1950) on the interrelations of certain analytic and synthetic phytosociological characters is potentially the cause of a certain amount of confusion. The statement concerns the relation of our results to Preston's (1948) log-normal population and has been interpreted to mean that we thought our results were a confirmation of the general validity of the log-normal population. While we are convinced of the value and general applicability of this type of population distribution in many ecological situations, we should like to make perfectly clear that our results concerning the interrelations of frequency and density were not dependent upon our use of a log-normal distribution; they, therefore, should not be construed as offering proof or confirmation of the log-normal universe. The general frequency-density interrelations are an application of the Poisson series and as such can be demonstrated in any kind of population, providing only that the individuals are distributed at random.

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BOOK REVIEWS

Sociological Human Ecology [1]

The study of human ecology has been approached through the established and traditional fields of biology (plant and animal ecology), geography, sociology, and anthropology. The only common thread developed thus far by students in these disciplines, however, seems to be that of preoccupation with environmental factors. Nevertheless, it is encouraging that more and more scholars in these fields are turning to an ecological point of view in developing their researches, and general principles are slowly emerging. Recently there has been published by James A. Quinn a synthesis of the field of human ecology as seen by the sociologists. The author states in his preface that "sufficient progress has already been made in human ecology to warrant a systematic, critical stocktaking of its accumulated data and theory." He begins with the simple definition that "human ecology studies relations between man and environment." In this book the author deliberately shapes his discussion around the sociological aspects of human ecology, attempting to outline principles of value to the sociologist and to those concerned with community planning.

Ecological terms and concepts such as invasion, succession, dominance, aggregation, web of life, niche, habitat, and gradient are defined and used in the book, although frequently they are somewhat modified to apply to human situations. The term "symbiosis" is used in such a way as to bear no relation to its use in biology. This, however, seems to be the only extreme case of such deviation. There has been a serious attempt to carry terms and concepts from plant and animal ecology into the sphere of human relationships in their original meanings as closely as possible. Many earlier writers used the expression "human ecology" only in the sense of spatial relations of man. Quinn not only outlines the spatial organization of human society but employs functional ecological concepts in explaining such organization and suggests practical application of the concepts in solving problems of areal structure. Occasional parallels are drawn between situations in human ecology and comparable ones in plant and animal ecology.

Citations are made to a very wide selection of publications from all fields of ecology—biological, geographical, sociological, and anthropological—but with emphasis upon those from sociology. References to literature in plant and animal ecology seem to serve the purpose for which they are cited, although this reviewer believes that frequently better selections could have been made.

Quinn's chief criticism of the biologists' attempt to study human ecology is stated as follows: "They look upon human ecology as an extension to man of general ecological concepts and principles. This point of view neglects completely the factor of culture, which makes human ecology differ in certain fundamental ways from plant and animal ecology." This sociological point of view, which certainly cannot be denied, is further stressed by the statement that "Scholars have agreed that culture plays a fundamental part in shaping the pattern of man's adjustment to environment." Nevertheless, the author makes a just tribute to Bews' classic book on "Human Ecology" with the admission that "J. W. Bews, a botanist, presents the most inclusive conception of human ecology found in ecological literature." However, some significant writings of several other biologists on human aspects of ecology have been overlooked, notably the works of Paul B. Sears.

Quinn's "Human Ecology" is divided into four parts. Part I contains introductory chapters on "The Field of Human Ecology" and "Adjustments of Man to Environment." Part II contains ten chapters devoted to "Structure and Planning of Areas." This is followed by the most truly ecological section of the book, Part III, consisting of five chapters on "Processes Underlying Areal Change." Part IV, with six chapters, is entitled "Interpretation of Spatial Distribution."

Practically every chapter ends with a selected bibliography of a broad nature with annotations on the nature and significance of each reference. There is a complete index at the end.

Social scientists have been guilty of using the expression "human ecology" in a vague and meaningless way. Quinn has made an effective advance toward synthesizing sociological studies which approach human studies upon a truly ecological basis.

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[1] **Quinn, James A.** 1950. Human ecology. 561 pp. New York: Prentice-Hall. $6.65.

Recent Textbooks of Human Ecology

"Man's place in nature" was discussed before Huxley's time, and human ecology is not a new subject. The role of environment in shaping human life, individual and social, cannot have lacked its paleolithic students, and "ecologic man" undoubtedly existed before "economic man" acquired an economy. The modern study of ecology as a formal discipline was cast in human terms long before Darwin and Warming drew biologists' attention to the facts of life; in a remarkable essay published in 1831, and republished in 1835 in the comprehensive work, "Sur l'Homme et le Développement de ses Facultés, ou Essai de Physique Sociale," Adolphe Quetelet, himself building on the work of the illustrious founders of the science of statistics, Graunt, Halley, Derham, and Süssmilch, bequeathed to his successors a philosophy, and what was of greater importance at the time, a methodology, of human ecology. "*The properties of the human species considered en masse*", said Quetelet (in italics), "*belong to the facts of physics;* the greater the number of individuals, the more is individual vagary subordinated to a series of general facts, facts attributable to the general causes, in accordance with which society exists and maintains itself. These are the causes we seek, and when we know them we shall know their effects on society, as we determine effects from causes in the physical sciences" (free translation).

There is little that is really new, then, in the works under review. What makes them of more than passing interest to ecologists is the occurrence of the term *human ecology* in their titles. There is no doubt that the term itself is new. Is it in fact just another name for sociology? Quetelet has some claim to the title of "founder of sociology," though the name he used was "social physics." The University of Cambridge has recently appointed a Professor of Human Ecology (A. Leslie Banks), but the authors of two of the three textbooks under consideration hold chairs of sociology in their universities. A publisher's representative, no more cynical than most of his fraternity, has remarked to the reviewer that the way to sell a textbook of sociology is to call it "Human Ecology." One may suspect that in the course of a long history of academic departmentalization, during which some "naturalists" have come to call themselves "ecologists" and some "political economists" have become "sociologists," sociology has rediscovered its roots in the biologic sciences, and borrowed a term to cover the new emphasis. The suspicion deepens into certainty with a reading of the new books. The re-orientation of thinking implied by the term "human ecology" has been healthy for social science, but if it is to be equally fruitful for general ecology one must be sure that ecologic concepts and terms are being correctly applied to the facts of human society. For this reason we shall be especially concerned with the scope of the books under review, for what they leave out tells us more about their authors' philosophic positions as ecologists than what they include.

James A. Quinn, in a work[1] that is reviewed in more detail elsewhere in this issue of Ecology, holds a view of the scope of human ecology that is at least explicitly stated, totally inadequate though it seems to the reviewer: "Because of its sociological [as distinguished from geographic or economic] orientation, this book emphasizes synecology almost to the exclusion of autecology. It deals primarily with areal patterns of group life, and especially with the sub-social aspects of community and regional organization" (p. 12). "This point of view omits all studies of the strictly social aspects of human interrelations. It emphasizes the point that the men and institutions of an area become integrated into a sub-social 'communal organism' as the result of impersonal 'competitive' processes" (p. 7). There is no doubt that this restriction makes the subject enormously easier to deal with, and as a result the book is a clearly written, informative account of certain aspects of human areology, particularly the factual background necessary for intelligent urban planning in 20th century United States.

One would learn very little of the nature of animal societies, however, if he restricted his studies to *Apis mellifica,* artificially maintained in "metropolitan" conditions in an apple orchard surrounded by clover fields, and remained satisfied with the discovery that the supply of honey shows a net gain only when the flowers visited are near enough so that more honey can be brought back to the hive than is utilized as fuel for flights. Such a student would be leaving entirely out of consideration (1) the nature of the mechanisms permitting social cooperation ("non-conscious cooperation", trophallaxis, communication systems, etc., in animal societies, "culture" in human societies), and (2) the comparative sociology of animals, i.e., the evolution of social mechanisms conferring increased efficiency in the exploitation of the habitat, and the reasons for the survival of comparatively inefficient species.

Quinn's omission of the "social" from an account of sociology, paradoxical though it is, is deliberate and understandable. Within the limitations he has set for himself, however, the lack of a comparative viewpoint is glaring.

[1] **Quinn, James A.** 1950. Human ecology. New York: Prentice-Hall. $6.65.

Virtually all the illustrations of regularities of urban growth and organization are drawn from U. S. cities; many of the statements made are probably not true of Latin-American cities, and their applicability to Ur or Uaxactun is extremely doubtful. Quinn's acount of "invasion" and "succession" in terms of sequences of land use in Chicago or Boston appears to be based on a purely superficial resemblance to processes known to plant ecology, for succession involves creation of new niches during the replacement of species by other species, and in its most useful sense implies a quantitative change in ecologic productivity. Primitive societies have doubtless succeeded each other in a more truly analogous sense, but in his preoccupation with the spatial distribution of certain elements of modern western civilization Quinn tends to forget primitive societies entirely; one strange result is the almost complete omission of any treatment of the biology of populations. These deficiencies are probably to be explained, though hardly to be excused, by the fact that comparative sociology is not sociology, as currently defined, but ethnology or anthropology.

Another book with the same title by Amos H. Hawley,[2] is much more satisfactory as a contribution to general ecology. To judge by the content of the four introductory chapters, which deal specifically with animal and plant ecology and the place of human ecology in the general framework of the subject, Hawley's reading in biology has been wider and deeper than Quinn's, and his view of human ecology is adequately inclusive: "The subject of ecological inquiry is . . . the community, the form and development of which are studied with particular reference to the limiting and supporting factors of the environment" (p. 67). "Human ecology . . . deals with the central problem of sociology, that is, the development and organization of the community" (p. 73).

Clearly perceiving that demographic dynamics are basic to an understanding of human interrelationships, Hawley devotes the second part of the book to "The Human Aggregate." Although the student of animal populations may find the chapters on population growth and population composition somewhat discursive and ill-adapted to synthesis into a broader treatment of population biology, this is largely the fault of the subject, which has gained enormously in content at the expense of clarity since Quetelet's day. The chapter on "Population Balance" is challenging and refreshingly free from the parochialism of U. S. sociology.

Hawley is less successful in the most difficult part of the book, when he considers "Ecological Organization," first in its static aspects (Part III), and then in terms of "Change and Development" (Part IV). These parts are introduced by boldly written, exciting chapters, but the factual material handled is much the same as in Quinn's book, so that the reader is guided, as by an enthusiastic but merciless guide, through a maze of detailed information on traffic volume, patterns of residential rent distribution, time-cost distance, etc., in the presentation of which the leading ecologic ideas seem to have been forgotten, along with the comparative viewpoint.

The book is subtitled "a theory of community structure," but the reason is not easy to find, for to label sociology "ecology" is not to provide us with a theory. Probably Chapter 12, "Community Structure", is intended as a theoretical treatment; for the reviewer it is the most provocative chapter. "The collective life of man, as of all other organisms, revolves simultaneously about two axes, one of which is symbiotic, the other commensalistic. The former pertains to the interdependence of unlike forms, i.e., units of dissimilar functions; the latter to the co-action of like forms, i.e., units of similar functions" (p. 209). Two kinds of groupings develop in consequence. (1) The *corporate* group, internally differentiated and symbiotically integrated, may be the indivisible unit of a society, though Hawley does not go so far as to say so. At any rate, the outstanding example of a corporate group is the family, and the biologic family is the basis of all known insect and primate societies. (2) The *categoric* group contains functionally undifferentiated individuals, related commensally; age groupings and occupational groupings are familiar examples, though labor unions, like other categoric groups, show a distressing tendency to become corporate.

Biologists may quarrel with the stretching of the terms "symbiosis" and "commensalism" to embrace these concepts, but the antithesis appears to be real, though occasionally difficult to discern in practice. If the two kinds of groups can be enumerated (and Hawley himself makes little effort to do so), this classification of social relationships might serve as a useful framework for generalization, if not precisely as a basis for a general theory of human society. Its mathematical development would not be excessively difficult; it would probably begin with the expression for the number of social contacts possible in a group

$$\frac{n^2-n}{2},$$

where n is population size. (This familiar relationship Hawley naively attributes to a writer in the *American Journal of Sociology*, 1945.) The next desideratum would be em-

[2] **Hawley, Amos H.** 1950. Human ecology. A theory of community structure. xvi + 456 pp. New York: Ronald Press. $5.00.

piric data on the number of corporate and categoric groups in a wide range of societies; such data doubtless exist already. As parts of the whole, their numbers will perhaps be found to exhibit heterauxesis with respect to n, but n will have to be carefully defined, presumably in ecologic rather than capital units. Before the ecologist rejects this approach as irrelevant, he should remind himself that in Sewall Wright's mathematical theory of evolution, the n term (the size of the breeding population) no longer appears impossible to measure in the field, as it did when it first emerged.

Training for rigorous mathematical thinking is largely being left out of the education of sociologists, if we may judge by Hawley's and Quinn's texts. The rejoinder, "*tu quoque*", may be dodged by stating at once that there are huge areas of biology into which mathematics cannot yet penetrate, and that the reviewer does not expect every new work of ecology to equal Lotka's "Elements of Physical Biology." The observation is made by way of introducting another "human ecology",[3] an extraordinary work by any standards but one that is fantastically different from the other two in its approach to the subject. Whatever the faults of Zipf's performance, and only a few of them can be discussed here, lack of appreciation of mathematics is not one of them. In fact, it suffers badly from the defects accompanying that very quality, for after a splendid beginning it degenerates into an exercise in special pleading for a particular mathematical device, regarded as a philosopher's stone. Probably this is an escape reaction, characteristic of a brilliant mind frustrated by the refractoriness of his research material and the unsympathetic attitude of his colleagues.

The author's attack on the problem of human social behavior is oblique but highly original: he begins with the study of speech. In certain extensive samples of "running speech", such as Joyce's "Ulysses", it is found that the frequency of occurrence (f) of words is related to their frequency · rank (r)

$$fr = C, \tag{1}$$

where C is a constant, the equation for a rectangular hyperbola. Moreover, the number of different meanings assignable to words is systematically related to the frequency of occurrence of those meanings

$$m_r = \sqrt{F_r}, \tag{2}$$

where m_r and F_r are the number of meanings and the frequency of occurrence of those meanings for any word whose frequency of occurrence has rank r. But ranks have integral values only, so that if F is the frequency of the most frequent word, F/r is the frequency of any word of rank r, and the terms in the equation form a harmonic series, $F/1$, $F/2$, $F/3$ . . . F/n, whose sum is a function of F:

$$F \cdot S_n = \frac{F}{1} + \frac{F}{2} + \frac{F}{3} \cdots + \frac{F}{n}, \tag{3}$$

where F is as defined, and S_n is the sum of n terms.

So far the treatment strongly resembles that of a difficult though not fundamental problem in ecology, the relation between the relative frequency of occurrence of the commonest and rarest species in a sample, as discussed by Fisher, Corbet, and Williams [4] and by Preston.[5] It turns out, however, that words have a property that can hardly be expected of species of moths falling into a light trap, namely, that the intervals between occurrences are related to the relative frequencies of occurrence

$$N^p \cdot I_f = K, \tag{4}$$

where N is the number of intervals of length I, I_f is the length of interval between occurrences of a word whose frequency of occurrence is f, and p and K are constants.

At this point some calculus would seem to be in order, but Zipf (perhaps because his book is intended for the general reader) turns to an elaborate model involving a demon required to ring bells arranged in a line, ringing one each second and ringing each bell with a frequency that is inversely proportional to the work involved in running to it and returning to the starting point. If the demon is also required to distribute his work evenly over time, i.e., to make the rate of work dw/dt a minimum, equations (1), (3), and (4) will be found to describe the frequency with which a given bell is rung and the length of intervals between peals. This means that the demon must have a clear perception of his future expenditure of effort, and implies further that in speaking human beings attempt to minimize their probable average expenditure of work (the "Principle of Least Effort").

In effect, the rest of Zipf's book is an attempt to apply these comparatively simple equa-

[3] **Zipf, George Kingsley.** 1949. Human behavior and the principle of least effort. An introduction to human ecology. xi + 573 pp. Cambridge, Mass.: Addison-Wesley Press. $7.50.

[4] **Fisher, R. A., Corbet, A. S., and Williams, C. B.** 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Jour. Anim. Ecol., 12: 42–58.

[5] **Preston, F. W.** 1948. The commoness, and rarity, of species. Ecology, **29**: 254–283.

tions to all human behavior, and to much besides. The hyperbolic relationship of equation (2) in particular implies a balance between a "Force of Unification" (the "speaker's economy" that attempts to put all meanings behind a single word), and a "Force of Diversification" (the "auditor's economy" that requires each meaning to be represented by a different word). Therefore, the concept of two opposing forces is painstakingly sought out in all relationships amenable to rank-frequency analysis, including the length of newspaper articles, the size of cities, and the number of species in a genus, to cite a few of the most interesting in an incredibly wide range of phenomena. The hyperbola becomes a touchstone capable of unlocking the mystery of the mind, and of evolution.

The fundamental fallacy, of course, lies in the application of mathematics to empiric data; there are many ways in which a hyperbolic relationship can be rationalized, but unlike the theoretical physicist Zipf never returns to question the assumptions on which his original inferences were based, and as a theory of human ecology (or of anything else except semantic balance) the work is a rococo house of cards, bathed in moonshine. Chapter 9, "The Economy of Geography," however, is recommended to general ecologists for its ingenious attempt to solve the problems of spatial relationships in inhomogeneous space, problems similar to those arising in biogeography [6, 7] and in plant ecology. The approach is like that of Stewart,[8] and deserves fuller exploration.

The range of human ecology is so enormous that the general ecologist finds it difficult to keep abreast of advances in its various subdivisions, let alone to relate them to his own researches in the comparatively simple sub-human world. Several other books have recently been sent to ECOLOGY for review. Two of them will be mentioned briefly here lest they be forgotten in the flood of literature that threatens to drown research.

An exceptionally successful attempt to deal with a restricted aspect of human ecology, the geographic aspect, deserves to be cited, for although it has been reprinted six times since 1934, without essential change, it is less well known among biologists than it should be. This is Forde's "Habitat, Economy, and Society," [9] a fascinatingly written mine of information. Frankly intended as a textbook, it is a remarkably lively one. No doctrinaire position of geographic determinism is taken, but it happens that the geographic background of human culture comes sharply into focus when primitive societies are considered, and the author makes the most of his opportunity to draw a coherent picture.

Laura Thompson's study of the Hopi [10] is a work of cultural anthropology, based primarily on a scientific probing of Hopi personality by a corps of psychologists and anthropologists. "Culture," or group personality, is considered to undergo ecologic succession, and the inherently balanced, logically and emotionally consistent social structure of the Hopi is believed to be "near climax." "Unlike those of plant and other animal communities, 'optimum' or 'climax' types of human communities are characterized not only by a high degree of organic integration within the total environment but also by a high degree of symbolic (logico-esthetic) integration within it" (p. 178). Acculturation, the cruelly difficult process that has brought the Hopi to their present crisis, is thus thought of as analogous to other forms of disturbance of the climax. As this admirable book makes clear, the general ecology of the Hopi, though viciously mismanaged in the recent past, is an eminently "manageable" problem in an academic sense, i.e., a scientist can hope to see it and think about it in its entirety, and administrative manageability should be within comparatively easy reach. What the Indiana Dunes were to Cowles, and the Galapagos to Darwin, the Hopi may be to the human ecologist, a naturally occurring laboratory model; or, as Birge once put it, referring to Lake Mendota, "infinite riches in a little room." The work is handsomely illustrated, and contains, as Chapter 8, a skillful *pasticcio* of the extraordinary writings of B. L. Whorf on the relation of Hopi language to Hopi intellect and personality.

Of what, then, does human ecology consist? To the reviewer, it is that fraction of general ecology that considers human beings; it therefore includes all the social sciences, even (unhappily) economics. Human biology in its autecologic aspects, including physiologic psychology, is a division of general biology, and, though basic to ecology as all biology is, does

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[6] **Ekman, Sven.** 1940. Begründung einer statistischen Methode in der regionalen Tiergeographie. Nebst einer Analyse der paläarktischen Steppen- und Wustfauna. Nova Acta Soc. Scient. Upsaliensis (4), 12, no. 2. 117 pp.

[7] **Webb, W. L.** 1950. Biogeographic regions of Texas and Oklahoma. Ecology, 31: 426–433.

[8] **Stewart, J. Q.** 1947. Empirical mathematical rules concerning the distribution and equilibrium of population. Geogr. Rev., 37: 461–485.

[9] **Forde, C. Daryll.** 1949. Habitat, economy, and society. A geographical introduction to ethnology. xv + 500 pp. London: Methuen; New York: E. P. Dutton. 7th ed. $4.50.

[10] **Thompson, Laura.** 1950. Culture in crisis: a study of the Hopi Indians. xxiv + 221 pp. New York: Harper and Brothers. $4.00.

not bring us to the essence of the discipline, which is the study of groups.

This being the case, it is clear that, wide as is the range of subject matter in the books under review, something is being left out of human ecology as currently investigated. Ecologic communities are organized by trophic relationships, and can be thought of as devices for delaying the degradation of free energy. The human race is part of the biosphere, and like all animal populations lives ultimately by grace of the photosynthetic ability of plants. The following calculation is not to be taken seriously in its details, but is intended to prod the human ecologists into taking a more fundamental view of their subject, for it seems to the reviewer that much of their work is concerned with externals. The "occupational pyramid," for example, has little real relation to the Eltonian pyramid. What is "man's place in nature"? Huxley gave a zoologist's answer; here an ecologist makes a stab at it:

The standing crop of human beings can be taken as 2.1×10^9 persons, and, assuming a mean longevity of 25 years, the rate of production is currently 8.4×10^7 persons per year. Correcting the mass of the average adult for the fraction of the average population that is of pre-adult age, we find an average mass of 60.55 kg., of which 35.7 per cent is organic matter. The energy content of this organic matter, most of which is protein with an energy content of 5.65 Cal./g., is 2150 Cal./kg., and the net production of chemical energy as human substance is therefore $(8.4 \times 10^7)\ (60.55)\ (2{,}150) = 1.09 \times 10^{13}$ Cal./year. About five times this amount, or 5.18×10^{13} Cal./year, is consumed in maintenance activities and does not appear as mass, so that the gross production of human substance is $1.09 + 5.18 \times 10^{13}$ or 6.27×10^{13} Cal./year.

Now the base of the human food chain is the production of plant organic matter, and this has been estimated by Noddack at 15.1×10^9 tons of organic carbon per year on the terrestrial part of the earth. If this be assumed to be all glucose, and therefore edible by herbivores, the net plant production in energetic units is 155×10^{15} Cal./year. The efficiency of human productivity is therefore $6.27 \div 15{,}500$, or 0.04 per cent.

This is a remarkably high value, and yet it is surely an underestimate, for the carbon produced by plants is not all glucose, nor is the whole terrestrial part of the globe available to grow human food; moreover the calculations do not allow for any appreciable storage of high-energy fat. Evidently a figure of 0.1 per cent would not be unreasonable for human ecologic efficiency.

An estimate of 10 per cent has long been considered as a fair approximation to the efficiency of herbivory, and primary carnivory may be assumed to have an equal efficiency. The theoretical maximum efficiency of primary carnivory, referred to the plant production, is therefore of the order of 1 per cent, and will not be very different (2 per cent) if carnivores are twice as efficient as herbivores. Thus, if man is a carnivore, he accounts for something like one-tenth of all the carnivory there is. His demands for food alone on the earth's annual increment of organic carbon are by no means a negligible factor in the economy of nature; his inroads on fossil carbon for industrial energy, and on living carbon for shelter and fuel, have been left out of account. Moreover, the human population today is certainly larger than it has ever been, and it is increasing by about 1 per cent per year, so that a tendency to shorten the food chain by becoming increasingly herbivorous seems inevitable, and with it must come an increase in the exploitation of the sea.

If this trial balloon draws the fire of the human ecologists, we may all learn something, and no one will be happier than the reviewer.

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Warfare as Group Sexuality [1]

The principal thesis of this curious book runs somewhat as follows: In *Pandorina* sexual activity totally disrupts the cell colony, and in all more complex associations, cellular or social, partially disrupts the aggregate. In human society the disruption in question is expressed in the Oedipus situation and primitively in sexual struggle between unmated young males and the old dominant mated males. Human warfare viewed abstractly as a biological movement of individuals, looks like a mass movement of microgametophores into a previously isolated population, with a subsequent impregnation of the female part of the invaded population. The function of wars and, one must suppose, of the other forms of foreign travel also, is firstly to lower Oedipal tension at home and secondly to promote panmixis abroad. The

[1] **Walter, Norman.** 1950. The sexual cycle of human warfare. Being a new theory of the cause of war and an inquiry into the possibility of war prediction. 207 pp., 11 figs. London: The Mitre Press. 15/–.

author is well aware that the process is getting out of hand. He feels rightly that nothing can be done to prevent this frightful hypertely until its causes are understood. He believes that these causes go so far back into the nature of sexual reproduction that only a really drastic cure such as the evolution of a non-sexual majority worker caste or the development of artificial parthenogenesis can produce a solution.

The book is marred by a somewhat diffuse and repetitive style and by a tendency to protest too much. It would also be a far more useful contribution if the author had shown more knowledge of the details of vertebrate behavior and of the immensely diversified ways in which various so-called primitive peoples have solved the kind of practical problem that he is considering.

Moreover, he hardly realizes the existence of women in human populations. Although the book is about sex, almost the only things which he lets us see he knows about women are that the "thought of large numbers of young men being slaughtered in the sexual prime of life is unquestionably exciting to many women," and that (from figure 11A), in a state of sexual anarchy without the regulating influence of wars, there would be one woman to every 3.7 men. It is obvious that, if one had a supply of women and an operational procedure for selecting those who were excited by the continued persistence rather than the slaughter of young men, one could work wonders merely by introducing rather more than 2.7 per man of the more attractive available women into the system. Even if it be granted that Mr. Walter's gloomy views on feminine sadism are partially correct, experience in any university town during the football season suggests that very few casualties in the symbolic war of the Bowl are really needed as a counterpoise to the attraction of real live young men in no imminent danger of death.

This conclusion, in fact, brings one to a major criticism of the book. The whole possibility of various forms of symbolic warfare, so successfully used by many birds for instance, is overlooked. By not indicating the existence of such possible ways of dealing with the problem of the book may, in spite of its originality and courage, do a disservice to thought on the matter. Mr. Walter's comparative psychology and anthropology are, in fact, wretchedly inadequate but the many Freudian insights into the behavior of Western societies, to which such insights best apply, make this work an essential, if minor, contribution to the study of the most important practical problem facing mankind to-day.

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"Ortstreue" and Subspecies Formation in the Pied Flycatcher[1]

Von Haartman has made a study in considerable detail of the population of pied flycatchers, *Muscicapa hypoleuca,* in a limited area in Finland over a period of eight years, using colored bands to identify individual birds in the field. In this paper he discusses their *Ortstreue* and its implications concerning the splitting of the species into subspecies. *Ortstreue* is the tendency of an animal to return to its birthplace or breeding place, particularly for breeding. The word "philopatry" will be used as its English equivalent in this review.

The study area consisted of a peninsula almost entirely surrounded by narrow straits on Finland's irregular southwest coast. Its area is about 3.9 square kilometers. Of this, about 3 square kilometers is covered with woods, mainly coniferous, but with deciduous trees scattered in the open parkland and on the forest borders. The pied flycatcher is euryoecous, nesting in nearly all the habitats present, except dense spruce woods, provided nesting cavities are present. Individuals nested in different habitats in successive years, as well as differing from each other in their preferences. They had the obliging trait of usually preferring boxes put up for them to natural cavities, when the two were side by side, even when courtship patterns involving the natural hole had been initiated. This of course made trapping relatively easy.

An important fact brought out by color-banding is the polyterritoriality of these birds. In addition to the regular nesting territory, von Haartman recognizes *Vorreviere,* territories abandoned by the males before nesting begins, and *Nebenreviere,* which the males often claim after their mates have begun to build their nests. Successive polygamy frequently occurs, a male leaving his first mate to pair in a *Nebenrevier* with a newly-arrived female or one who has lost her first clutch. The males usually return to feed the first brood rather than the second. This polyterritoriality made the study difficult, since one territory might be within the study area and another outside it.

The data which form the chief basis for this

[1] **von Haartman, Lars.** 1949. Der Trauerfliegenschnäpper. I. Ortstreue und Rassenbildung. Soc. pro Fauna et Flora Fennica, Acta Zool. Fenn. **56**: 104 pp.

TABLE I. *Returns of banded Flycatchers to the banding place*

	Adult males			Adult females			Young		
	Returns (number and percentage)		Further studied	Returns (number and percentage)		Further studied	Returns (number and percentage)		Further studied
Originally banded			189			177			851
First year after banding	70	37.1%	59	19	10.7%	13	9	1.1%	9
Second year	26	44.7%	21	7	53.8%	5	4	44.4%	3
Third year	10	47.6%	8	3	60%	2	1	33.3%	0
Fourth year	4	50%	4	0	0%				
Fifth year	3	75%	1						
Sixth year	0	0%							

paper are the return data. The percentage returns are calculated as 100 times the number of birds which return to the study area in one or more later years, divided by the total number banded. This formula does not give as accurate a picture as one which takes into consideration the number of times an individual returns, but for the purposes of comparison with the birds banded as fledglings and indicating changes in the returns of later years, it is preferable in this case. These data are presented in Table I. The discrepancy between the returns for a given year and the number further studied is due to the fact that some birds returned the last summer of the experiment and could not be further studied for this report. According to Drost and Schilling (Ber. Ver. Schles. Ornith. **40**: 71–85, 1940), and to earlier studies by von Haartman, about 40% of the second-year birds and 23% of the young birds of this species survive the winter. It appears then, that if these survival figures are applied to this population, virtually all the surviving males (37.1%) return to the vicinity of their last nesting place, while less than one third of the surviving females (10.7%) do so. However, of the birds which have already returned once, the percentages which return for the second and following years after banding are about the same for both sexes and appear to increase slightly as the birds get older, although the samples are too small for this increase to be considered significant. Likewise the sample of young birds which returned to their birthplace is too small for its sex ratio to be significant, but it is interesting to note that seven of these nine were males, again showing about three times as many philopatric (ortstreue) males as females. It is quite common among birds, according to von Haartman, for the females to be somewhat less philopatric than the males, but only in the prothonotary warbler is the difference known to be as great as in the pied flycatcher. The distance between the nesting sites of successive years is also somewhat greater for the females.

According to the return data above and the above-mentioned winter survival percentages, and assuming a 1:1 sex ratio among young birds, von Haartman classifies the pied flycatcher individuals on the basis of philopatry into the following categories:

Males

1. Return each year to the birthplace—7% (7 out of 98 (23%) survivors of 425 young males).
2. Leave the birthplace, but return each year to the first nesting place—93% (the remaining male survivors).

Females

1. Return each year to the birthplace—2% (2 out of 98 (23%) survivors of 425 young females).
2. Leave the birthplace, but return each year to the first nesting place—37% (explanation below).
3. Nest in a different place each year—61% (explanation below).

The 98% of the females which do not return to the birthplace are divided on the basis of the total percentage returns, counting a bird which returns twice to breed after being banded, as two returns out of two bandings, and so on. In the case of these females, this formula increases the return percentage from 10.7% to 14.7%, which is 37% of the 40% which are estimated to survive each winter. The remaining 61% apparently nest in a different locality each year. There might be some intermediate individuals which nest in different places for the first two or more years and then settle down in one place, but this seems unlikely in view of the fact that the distance between nesting sites of a given individual in successive years, as shown by the philopatric birds studied, does not decrease as the birds grow older. In any case, the birds are so short-lived that such

wanderers would generally be indistinguishable from non-philopatric ones.

Von Haartman considers the philopatric quality to be inherent in the birds which possess it, rather than due to greater success in competition for territory, because combat is unusual in the females and unsuccessful attempts to settle were much more common in males than in females. Furthermore, the dates of arrival and egg-laying of philopatric females were not significantly earlier than those of the others. Apparently the non-philopatric adult females lack a genetically-controlled factor which makes their home-loving sisters try to settle in a familiar place. The author suggests that philopatry may be a recessive character, because six offspring of 196 banded philopatric females returned to the area, while only three offspring of the 632 non-philopatric females returned. This information is too meager to permit drawing any definite conclusions, but it certainly seems to support the hypothesis that philopatry is genetically determined. That environmental factors affect it is indicated by the data on returns by birds which have lost a brood. Such a loss apparently reduces the tendency of females to return to the previous year's nesting locality, but does not affect the males.

The third chapter of this report discusses von Haartman's results in comparison with those of people who have worked on *M. hypoleuca* in Germany. These German birds are considered to be a different subspecies, because they average lighter in color. The central European birds gave a higher percentage of returns than those of Finland. In Germany, the young are more philopatric and the females behave more nearly like the males in this respect. In fact, the presence of non-philopatric females in Germany is doubtful. The author makes a good case for his belief that the differences between the races is inherent in the animals themselves and not the result of environment. The postglacial creation of new areas suitable for invasion would operate selectively in favor of the non-philopatric character, and it then would be logical to expect a higher incidence of this character in the more northern subspecies.

In Chapter IV other species are compared with the pied flycatcher. Banding studies in Europe and America have shown the percentage returns of various species, and data on the distance of the point of recovery from the point of banding can form a basis for comparison of the dispersal distances of different species, although such data must be interpreted with great caution, when work done by different people is compared. For example, colored bands, eliminating the necessity of retrapping for identification of individuals, will give a greater percentage of recoveries, but only in a limited area. Von Haartman has tried to make the data for different species comparable as much as possible, but the difficulty of doing this is illustrated by the fact that he gives the greatest dispersal distance of the American robin as 425 kilometers, when it should be 425 miles. In all the species studies, the percentage of returns of birds banded as adults is much greater than that of young birds, which only exceeds 10% in three of the 19 species studied, while the percentage of adult returns is over 20% in nearly all. But it is very hard to assess how much of this difference is due to stronger philopatry, how much to learning navigation, and how much to increasing winter survival, as the birds grow older.

It is obvious that philopatry or the lack of it must play an important part in the expansion of the range of a species. Such expansion is apparently spearheaded by birds of the previous year and older females. From the German data, von Haartman has calculated the mean distance of a generation's nesting places from its birthplaces. It appears to this reviewer that he has used the upper limits rather than the midpoints of classes in this calculation, in which case his figure of 4 kilometers is too high. Using this figure, D, in the formula $D\sqrt{n}$ where n is the number of generations, in this case estimated at 13,500, since the maximal glaciation, the mean distance of the present-day breeding-places of pied flycatchers is about 464 kilometers from the breeding-places of their ancestors of 23,000 years ago. This assumes a continuous expansion in a uniform medium, which has obviously not been the case. As the author points out, these calculations are based on the average dispersal distance between generations; individuals often go much farther. Furthermore, these are the relatively philopatric German birds, not the Finnish ones, which form the vanguard and should therefore give a truer picture of the rate of expansion.

The conclusion from all this is that the degree of philopatry is an appreciable factor in postglacial expansion, but that overcrowding or other external factors may also play a part. In this connection von Haartman points out that of six species of passerine birds in which the dispersal distance has been calculated, the two with the shortest distances nest in the open, while the others all nest in holes, suggesting that the availability of nesting sites may be an important factor in selection for or against philopatry.

In his last two chapters the author discusses the relationship of philopatry to subspecies formation. *Muscicapa hypoleuca* has four subspecies, one in eastern Germany and Poland, one in Spain and Portugal, one covering most of the rest of Europe east to the Urals, and one in North Africa. The closely-related collared flycatcher, *Muscicapa albicollis,* has two sub-

species, one extending from Germany and Italy to the Crimea, and the other from Greece and the east shore of the Black Sea to northwestern Persia. These subspecies differ mainly in the colors of the male's plumage, which also darkens with age. The author emphasizes philopatry as a factor promoting isolation, especially in cases where isolation is believed to have arisen through distance alone. Using the previously-discussed dispersal figures, he calculates the size of the panmictic area, and using census figures, he compares the estimated population of the panmictic area with that of the total range of *M. hypoleuca.* The ratio is about $1:10^5$. The panmictic unit is of the order of magnitude of 215 pairs of birds. Under these conditions, according to Wright (Genetics **28**: 114–138, 1943), random variation in gene frequencies must be slight. But selection, uneven distribution, and occasional long range dispersal can still cause differentiation. A comparison of the degrees of philopatry of six species with the corresponding mean subspecies ranges hints at a tendency for the more philopatric species to split up into more subspecies. However, it should be pointed out that in the most philopatric species, the song sparrow, *Melospiza melodia,* the work was done on a subspecies with a very large range, and that the small mean subspecific range of this species is mainly due to its occupation of certain regions cut up by many topographic barriers.

This paper represents a great deal of intensive study and is a valuable contribution to our knowledge of the phenomenon of philopatry in birds. It is regrettable that a few errors were allowed to creep in, but these do not seriously detract from its value. Much of von Haartman's speculation admittedly ignores important factors and should not be relied on heavily for further speculation. But it is stimulating material and should provoke more thought and research on the problems with which it deals. In my opinion, its chief contributions are in illustrating again the value of color-banding over a period of several years and in showing the differences in philopatry associated with differences in age and sex.

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EXPERIMENTAL DESIGNS [1]

The authors have guided themselves first by the needs of an investigator preparing a new experiment. The designs are selected for their usefulness, and their relative advantages are expertly discussed. Directions for the experimental plans and the entailed arithmetic are verbally at a minimum, but logically complete. This should be a very good handbook in executing the designs it describes.

For one who is not a specialist in experimental designs, the selection of genus and species of the correct design to fit a contemplated experiment resembles the identification of an unfamiliar organism. A key is suggested below to the classification of designs used in this book. The characters chosen for classifying experiments are familiar by other names, and may need a word of identification.

Experimental units are elements of the material from each of which one observation is to be obtained. These units may be grouped according to two different principles. First, a certain uncontrolled variable or a number of variables may be expected to have effects on the observations. Groups of units equivalent with respect to these variables are called *blocks.* Ideally, experimental comparisons would always be made on units within a single block. Secondly, experimental units may be submitted to several *treatments* (including controls) whose differing results are to be compared.

Depending on the number of uncontrolled factors defining the blocks, an experiment may have a *single restriction* or *grouping,* a *double grouping* as when differences both of age and weight are eliminated from comparisons, or a *triple grouping.* Further, if the treatments are applications of several factors in all possible combinations, the experiment is called *factorial.* The separate effects of single factors are *main effects* and the dependence of the effects of certain factors on the presence or absence of combinations of the others are *interactions.*

If an experiment with t treatments has at most k individual units per block and if $t > k$, then not all treatments can be performed on a single block. This will be an *incomplete block* experiment. It may be that a certain treatment will be applied to every unit in one block and to none in another. Then the comparison of presence and absence of this treatment is *confounded* with the difference between blocks. In an incomplete block experiment confounding is always present but may be used for different purposes. Main effects of secondary interest or interactions suspected not to be important are often completely confounded, and designs are

[1] **Cochran, William G., and Gertrude M. Cox.** 1950. Experimental designs. 454 pp. New York: John Wiley & Sons; London: Chapman & Hall. $5.75.

KEY TO CHAPTERS 4–13

1. $t = k$ 2
   $t > k$ 3
2. Basic designs. Environmental variability and its elimination ..... *Chapter 4*
   Completely randomized designs ..... *Section 4.1*
   Grouping by one environmental variable. Randomized blocks ..... *Section 4.2*
   Double grouping. Latin squares ..... *Sections 4.3 and 4.4*
   Triple grouping. Graeco-Latin squares ..... *Section 4.5*
   Comparisons among treatments when the latter are combinations of several factors at selected levels. (Applicable equally for $t > k$.)
   Factorial designs ..... *Chapter 5*
3. Factorial experiments with confounding of certain interactions 4
   Factorial experiments with certain main effects confounded. Split plots ..... *Chapter 7*
   Experiments with no treatment comparisons completely confounded 5
4. Designed as randomized blocks. Confounding ..... *Chapter 6*
   Designs with double grouping. Quasi-Latin squares ..... *Chapter 8*
5. Incomplete blocks, general discussion and comparison, with an index to later chapters ..... *Chapter 9*
   Detailed incomplete block designs 6
6. Designs requiring $t = k^2$, $t = k(k+1)$ or $t = k^3$ 7
   Designs not requiring these relations 8
7. Designs with one environmental grouping. Lattices ..... *Chapter 10*
   $t = k^2$ ..... *Section 10.1*
   $t = k(k+1)$. Rectangular lattices ..... *Section 10.3*
   $t = k^3$. Cubic lattices ..... *Section 10.4*
   Designs with double groupings. Lattice squares ..... *Chapter 12*
8. Designs with single grouping. Incomplete blocks ..... *Chapter 11*
   Designs with double grouping. Youden squares ..... *Chapter 13*

also available which confound different treatments between different blocks so as to reduce the information on all treatments equally.

The presentation of each type of design includes, usually under well-marked section headings, (a) description, usefulness and comparison with other available designs, (b) arrangement of experimental material making the best use of its uniformity, (c) directions for randomization, (d) directions for the statistical analysis, including the necessary repairs for missing values, and (e) worked numerical examples. Following many chapters is a catalogue of plans, arranged by values of t and k.

Chapter 3 summarizes the principles and the algebra required in common by later particular designs. Subjects developed here are the least squares estimation of treatment effects, the notion of significance tests and confidence intervals, the t-test in particular, the method of analysis of variance with the logical assumptions upon which it depends, the isolation of orthogonal treatment and error components, the replacement of missing values and the analysis of covariance. This is a great deal to disclose at once to the beginning reader, but as an organized reference for notation, formulae and methods required later on the chapter needs no apology. The exposition is connected by a single numerical example in randomized blocks, which is made to illustrate the object and methods of each section. This economical approach gives insight into the algebraic manipulations, and perhaps a deceptive sense of mastery of the resulting general formulae.

An introduction is offered, in Chapter 14, to the logical problems of combining separate experiments, such as the use of weights in comparing results of unequal precision. Finally, a set of tables described in Chapter 15 provides 1,000 random permutations of the numbers 1 to 9 and 1,000 more of the numbers 1 to 16. Random permutations are more direct than tables of random digits in scrambling the order of N objects, which is the operation usually required in planning a design.

After becoming familiar the book should be a convenient reference. The notation and methods of Chapter 3 are presupposed in later chapters, so that it is necessary to learn where to check relevant formulae. The numerical examples, however, illustrate all new methods of computation, so that one can verify his mastery of the techniques. As to its possibilities as a textbook in a college course the authors point out from their own experience that (1) a more systematic development of the analysis of variance may be needed, (2) examples in fields familiar to the students are desirable (those included come particularly from agricultural research), and (3) more material is given than can be covered in a one-term course.

Because of its organization, the book presents

in a clear way what experiments best fit a given design. One is left to infer what designs best fit a given experiment. Though summary classifications (*e.g.,* those on pp. 151–2 and pp. 270–273) show the design possibilities in broad perspective, the problem of their detailed taxonomy has not been completed.

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What Is "Molecular Ecology?" [1]

"Problems of Morphogenesis in Ciliates" consists of a complete and fascinating review of the form changes that occur in the life cycles of certain parasitic ciliates, written from the standpoint of the problem of "molecular ecology."

While Lwoff's book is not intended primarily for the ecologist there are certain aspects of his work, and of the work of all those workers in embryology and associated fields who discuss "molecular ecology," that might well be examined by the ecologist.

When the terminology of one discipline is adopted by the workers in another two attitudes are common among the workers in the "parent" field. The first is a feeling of proper parental pride, usually phrased in the form "it's about time we finished this unending specialization and got down to general notions that apply to both our fields." The second reaction usually takes the form "of course you can't expect these barbarians really to do something useful with our ideas. After all, they did get them second hand."

If we assume that these things have been said, in one way or another, we are left with the problem: "what, if anything, can the ecologist derive from this partnership?" or, to phrase it differently, "is this symbiosis or parasitism?"

Both mature ecologists and adolescent Samoans will often seek to evade responsibility by the cry "Laititi a'u" ("I am but young"). It therefore seems somewhat startling that a venerable field such as embryology would find anything in the discipline of the ecologist that would be of any value.

The generalizations of "molecular ecology," as stated by Weiss [2] and quoted by Lwoff, are of the broadest possible sort. To paraphrase and condense the original statement by Weiss, they are essentially these:

1. There is a set of definable conditions, at a particular spatial region, independent of the entity itself, that will determine the probability that a biological entity (organism, plasmagene, enzyme, etc.) will continue to maintain its integrity in that region at some time subsequent to its introduction therein.

2. Interactions exist within and between biological entities, such that in any given spatial region laws can be found relating the past state of the system (in regard to number and kind of entities and the "probability determining conditions" referred to above) to its present and future states.

3. The conditions and interactions mentioned above may be such as to permit the region under consideration to be in equilibrium, or to be approaching equilibrium, or to be maintaining a dynamic state that will eventually result in the disappearance of one or more of the biological entities involved.

It seems very probable that the three statements listed above define the class of admissible laws of the science of ecology. They are not themselves empirical laws except in a rather peculiar sense. That is to say, we can construct a mathematical expression for the growth of a population of *Daphnia obtusa,* or we can construct a verbal description of the outcome of competition between *Tribolium confusum* and *Tribolium castaneum,* and such an expression or description would constitute an ecological law. These examples are admissible as *ecological* laws since the biological entities that are mentioned and the spatial regions in which they are maintained will behave in the manner indicated by the statements defining the class of such laws. The definition of the class of ecological laws will not itself predict the outcome of competition between species of flour beetles, nor will it predict the behaviour of any specific biological entities in any defined spatial region.

In order that "molecular ecology" can be used to discuss embryology it remains to be demonstrated that there are sub-organismic entities capable of obeying the kind of laws admitted by the formulation. The genes, for example, are not admissible without many careful stipulations regarding the spatial region being considered. That is, the notion of "introducing" genes into a given geographic region (see statement 1 above) can only be discussed with an exact picture of the organism containing those genes acting as some sort of intermediary between the genes and the region in question.

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[1] **Lwoff, Andre.** 1950. Problems of morphogenesis in ciliates. ix + 103 pp. New York: John Wiley and Sons, Inc. $2.50.

[2] **Weiss, Paul.** 1947. The problems of specificity in growth and development. Yale Jour. Biol. Med. **19**: 235–278.

Lwoff's work consists of showing that the kinetosomes of ciliates (the visible, self-reproducing granules associated with the cilia) are admissible entities. While some observational generalities are drawn relating to their behaviour in the life cycle of different ciliates, there are no laws constructed describing their interactions with each other or with specific environmental (*i.e.*, non-kinetosome cytoplasmic) factors. It is however indicated by the material presented in this book that such laws in all probability do exist.

From the viewpoint of Lwoff, Weiss' formulation has predictive value in that the existence of suitable entities is implied. The ecologist, on the other hand, has no doubts as to the existence of the organisms (*i.e.*, entities) that he is discussing. It is the laws relating to the interactions of these organisms that form the subject matter of ecology.

The work of Lwoff demonstrates the method by which a method for forming laws is brought into contact with the laws themselves. It is of interest to the ecologist as it demonstrates that the definition of the class of ecological laws has an existence independent of the laws themselves. The "molecular ecologist" will not usurp the laws of ecology, and what is taken as the foundation of "molecular ecology" ought not to be confused by the ecologist with the laws that he is trying to discover.

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Handbook of North Dakota Plants

This handbook[1] of Pteridophytes and Spermatophytes represents a landmark in the study of the botany of North Dakota. For a period of 40 years Professor O. A. Stevens has accumulated the requisite materials for a complete and useful flora. The book has reduced to a minimum those technicalities necessary to a proper understanding of the plant life of one of our most interesting prairie states. One finds this to be a manual with workable keys, neatly illustrated, and packed with facts about native and introduced plants. The handbook is printed on excellent paper and is substantially bound.

Concentrated in the forepart of the book are to be found introductory discussions on plant collectors in North Dakota, plant names, physiography, plant characters, and two family keys with instructions on how to use them. The first is a short key to the more common families; the second is a longer illustrated key which includes all families represented in the book. These aids to plant study, often illustrated by accurate line drawings, are useful to a beginner and constitute a pleasing feature for the professional. The physiographical features of the state are presented in lucid style. The summary of soils, ecological relations, vegetation types, and plant distribution is the result of many years of painstaking field work throughout the state.

In the taxonomic portion of the treatise, the author refers not only to the frequency and distribution of species in the state but often includes ranges outside the state. Pertinent remarks on affinities and plant distribution are given in the text. Toward the close of the descriptions of the species, the author generally gives useful data regarding blossoming time, fruiting time, and habitats. He also includes helpful notes concerning poisonous, useful, and introduced plants. The assistance of specialists in some groups is fully acknowledged.

In North Dakota where altitude ranges from 789 feet at Pembina, Pembina County, in the northeastern corner of the state, to 3,468 feet at Black Butte, Slope County, in the southwestern part of the state, there is not the diversity of vegetation types that is encountered in regions of greater altitudinal range. In spite of this, minor elevations influence soil moisture and have a profound influence on where plants grow. The author points out the predominance of prairie species. There is a limited amount of woodland along streams and a small forested area in the Turtle Mountains and Pembina hills in northeastern North Dakota. Devils Lake in Ramsey and Benson Counties is highly alkaline and, with smaller lakes and ponds with similar alkalinity, supports a limited but characteristic group of chenopod and other plants of alkaline habitats. The unglaciated region west of the Missouri River in addition to supporting many generally distributed plants is the locus for a goodly number of southwestern and Rocky

[1] **Stevens, Orin Alva.** 1950. Handbook of North Dakota plants. Fargo, North Dakota: Sponsored and published by the North Dakota Institute of Regional Studies. Pp. 1–324, 1 colored plate, 319 figures, species distribution maps. $4.50 at the Institute.

Mountain forms. The North Dakota flora as presented contains 1143 species. Dr. J. Lunell in his 1915–1917 enumeration of North Dakota plants listed 1,311 species and varieties. Professor Stevens indicates that many of the Lunell plants are only minor variations of older species.

In the handbook numerous recent taxonomic studies are incorporated. However, some species and varieties are omitted and a few untenable names are used. Some notable omissions from the book suggest that some important sets of North Dakota plant collections on file in the Herbarium of the University of Minnesota may not have been consulted. This is understandable when one considers the almost impossible task of gathering together all available data concerning the floristics of a state, including published records and information about plant specimens deposited in diverse herbaria.[2] The following is given to aid those who may wish to compare phytogeographical areas. A few notes relative to nomenclature and a few species which might possibly be added to the flora of North Dakota are recorded below.

A group of aquatic plants not given in the manual is recorded from North Dakota by W. C. Muencher.[3] These are *Potamogeton amplifolius* Tuckerman, *P. berchtoldi* Fieber, *P. foliosus* Rupr., *P. praelongus* Wulfen., *P. strictifolius* Benn., *Sparganium angustifolium* Michx., *S. chlorocarpum* Rydb., *Lophotocarpus calycinus* (Engelm.) J. G. Smith, and *Anacharis canadensis* (Michx.) Planch.

An error on page 11, map 9, under the caption of White Larkspur reads *Aquilegia;* this should of course read *Delphinium.* Printer's errors seem to be very few.

Because of the inclusion of soil reactions and relations, ecological habitats and plant distribution, comments on introduced plants, and systematic keys and descriptions with some dis-

[2] Professor Olga Lakela, University of Minnesota, Duluth Branch, informs me that her collection of some 600 plants from the vicinity of Minot, North Dakota, is on file at the State Teachers College at Minot with a duplicate set at the Herbarium of the University of Minnesota. The herbarium of Dr. J. Lunell is also available at the University of Minnesota Herbarium.

[3] **Muencher, Walter Conrad.** 1944. Aquatic plants of the United States. Comstock Publishing Company, Inc. Ithaca, New York.

Additional species not mentioned in the book, but known to occur in North Dakota

Name	Locality	Collector and year
Potamogeton richardsonii (A. Benn.) Rydb.	Fish Lake	Brannon 1896
	Leeds	Lunell 1901
	Lake Metigoshe	Bergman 1912
	Kulm	Brenckle 1914
	Minot	Lakela 1930
Potamogeton friesii Rupr.	Lake Ibsen	Lunell 1899
Cerastium arvense L. var. *viscidulum* Gremli[4]		
Polanisia trachysperma T. and G.	Leeds	Lunell 1908
	Devils Lake	Bergman 1912
	Marmarth	Stevens 1918
	Minot	Lakela 1930
Gentiana macounii Holm.[5]		
Gentiana tonsa (Lunell) Victorian[6]		
Cuscuta cuspidata Engelm.	Towner	Lunell 1908, 1918
Cuscuta umbrosa Beyrich ex Hooker	Dunseith	Lunell 1907
	Minot	Lunell 1905, 1908
	Peninsula of Lake Ibsen, Benson County	Lunell 1909
	Turtle Mountains, St. John	Lunell 1912
	Jamestown	Lunell 1913
	Pleasant Lake	Lunell 1914
Physostegia formosior Lunell	Minot	Lunell 1908
	Towner	Lunell 1908
Galium verum L.[7]	Dickenson	Waldron
Antennaria aprica Greene	Leeds	Lunell 1899, 1900 and 1910
Antennaria aprica Greene var. *aureola* (Lunell) J. W. Moore	Butte, Benson County	Lunell 1902

[4] Rhodora **50**: 214. 1948.
[5] Gray's Manual, ed. 8, p. 1160. 1950.
[6] Cont. Bot. Univ. Montreal, No. 20: 14. 1932.
[7] Lunell, J. Enumeratur Plantae Dakotae Septentrionalis Vasculares. I–XIII. Am. Mid. Nat. **4** and **5**: 1915–1917.

Species whose names should be altered for nomenclatorial reasons

Name used in book	Name that should be applied	Citation
Andropogon furcatus Muhl.	*Andropogon gerardi* Vitman	Summa Pl. 6: 16. 1792
Sisyrinchium graminoides Bicknell	*Sisyrinchium angustifolium* Miller	Gard. Dict. ed. 8. 1768
Sisyrinchium angustifolium	*Sisyrinchium montanum* Greene	Pittonia 4: 33. 1899.
Polygonum natans L. forma *hartwrightii* (A. Gray) Stanford	*Polygonum amphibium* L. var. *stipulaceum* Coleman	Cat. Fl. Pl. Pen. Mich. 32. 1874.
Chenopodium gigantospermum Aellen	*Chenopodium hybridum* L. var. *gigantospermum* (Aellen) Rouleau	Nat. Canad. 71: 268. 1944.
Salsola kali L.	*Salsola kali* L. var. *tenuifolia* Tausch.	Flora, Band 1: 326. 1828.
Nuphar advena (Ait.) Ait. f.	*Nuphar variegatum* Englem.	*in* Peck, Ann. Rep. Univ. of N. Y. 19: 73. 1866.
Arabis hirsuta (L.) Scop.	*Arabis hirsuta* (L.) Scop. var. *pycnocarpa* (M. Hopkins) Rollins	Rhodora 43: 318. 1941.
Geum canadense Jacq.	*Geum canadense* Jacq. var. *camporum* (Rydb.) Fernald and Weatherby	Rhodora 24: 49. 1922.
Impatiens biflora Walt.	*Impatiens capensis* Meerb.	Afb. Zeldz. Gewass. 10: 1775.
Vitis vulpina L.	*Vitis riparia* Michx.	Fl. Bor. Am. 2: 231. 1803.
Elaeagnus argentia Pursh	*Elaeagnus commutata* Bernh.	Allg. Thuer. Gartenz. 2: 137. 1843.
Circaea quadrisulcata (Maxim.) Franch. and Sav.	*Circaea quadrisulcata* (Maxim.) Franch. and Sav. var. *canadensis* (L.) Hara.	Rhodora 41: 387. 1939.
Convolvulus sepium L. var. *repens* L.	*Convolvulus interior* House	Bull. Torr. Bot. Club 32: 140. 1905.
Phlox pilosa L.	*Phlox pilosa* L. var. *fulgida* Wherry	Bartonia No. 12: 47. 1931.
Scutellaria galericulata	*Scutellaria epilobiifolia* Hamilton	Mon. Gen. Scut. 132. 1832.
Plantago elongata	*Plantago pusilla* Nuttall	Gen. 1: 100. 1818.
Kuhnia eupatorioides L.	*Kuhnia eupatorioides* L. var. *corymbulosa* Torrey and Gray	Fl. N. Am. 2: 78. 1841.
Aster paniculatus Lam.	*Aster simplex* Willd.	Enum. Hort. Berl. 887. 1809.
Tragopogon dubius	*Tragopogon major* Jacq.	Fl. Austr. 1, tab. 29. 1773.
Taraxacum laevigatum	*Taraxacum erythrospermum* Andrz.	*in* Bess. Enum. Pl. Vilh. 75. 1821.

cussions of pertinent taxonomic problems, this work should be of interest to ecologists, plant geographers, and nature study groups, as well as plant taxonomists. The handbook should find a place in the libraries of schools and persons interested in the flora of North Dakota. The citizens of the state can be proud of the Handbook of North Dakota Plants.

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BOOK NOTICES

Australia, Commonwealth Scientific and Industrial Research Organization. 1950. *Australian Journal of Marine and Freshwater Research,* Volume 1, Number 1. 154 pp. 7/6 per issue. An important new journal, to be published irregularly, makes its appearance with seven articles, three on the biology of marine fouling and four on marine fisheries topics. The journal is edited by N. S. Noble, and subscriptions will be taken by the Secretary of the Organization; both may be addressed at 314 Albert Street, East Melbourne, C.2, Victoria. *E. S. Deevey.*

Brown, F. A., Jr. (ed.). 1950. *Selected invertebrate types.* xx + 597 pp. New York: John Wiley and Sons. $6.00. This admirable practicum for both student and investigator provides a wealth of information on the general biology as well as the gross and microscopic anatomy of about 120 representative North American invertebrates. Prepared at the Marine Biological Laboratory, Woods Hole, Massachusetts, it places relatively little emphasis on the terrestrial arthropods. Authoritative, extensively and admirably illustrated, this is a valuable reference volume for the ecologist's bookshelf. *J. L. Brooks.*

Buxton, John. 1950. *The redstart.* (New Naturalist Monograph.) xii + 180 pp. London: Collins. 12 s. 6 d. The author of this delightful and well-illustrated monograph, a worthy member of a series that represents an outstanding venture in publishing, is a poet, scholar, and amateur ornithologist. For five years he was a prisoner of war in Germany, and with the help of fellow-prisoners undertook the kind of study of a single species, of a few individuals in fact, that is so much needed and that so few people have the leisure to carry out. To say that the book is a tracing of David Lack's "Life of the robin" on a more modest scale is intended as high praise. The circumstances of the study precluded experiments with redstarts; this is a pity, for many of the observations cry out for experimental amplification. Especially is this true of the "white feather in nest" situation (p. 67): a white feather is removed from the nest by cock or hen, apparently under the impression that it is a fecal sac, while the same feather outside the nest is treated by the hen as potential nesting material. Evidently the mind of the bird perceives the nest + white object as a "Gestalt," but verification is needed. *E. S. Deevey.*

Canada, Department of Resources and Development, Canadian Wildlife Service. 1950. *Wildlife Management Bulletin.* Ottawa: Canadian Wildlife Service. This is an occasional publication in processed format, inaugurated in 1950. Requests for copies should be addressed to the Service; no charge is made for them. Series 1, to be devoted to mammals, begins with "The mammals of Waterton Lakes National Park," by A. W. F. Banfield. Series 2, on birds, has as its Number 1 "A study of bird populations in the apple orchards of the Annapolis Valley, Nova Scotia, with particular reference to the effects of orchard sprays upon them," by John P. Kelsall. Series 3, on aquatic wildlife, opens with two papers by Victor E. F. Solman (No. 1), "Prince Albert National Park creel census analysis, season 1948," and (No. 2) "Limnological investigation of Fundy (New Brunswick) National Park, 1948." *E. S. Deevey.*

DeBeer, Edwin J. (ed.). 1950. *The place of statistical methods in biological and chemical experimentation.* Ann. N. Y. Acad. Sci., **52** (6): 789–942. $2.25. This series of fifteen papers with an introduction by the editor is the result of a conference held in January, 1949. Both general principles and detailed applications are discussed. Ecologists may be particularly interested in a paper by Frank Wilcoxon, "Some rapid approximate statistical procedures" (pp. 808–814). *E. S. Deevey.*

Farris, Ermond J. (ed.) 1950. *The care and breeding of laboratory animals.* xvi + 515 pp. New York: John Wiley & Sons; London: Chapman & Hall. $8.00. Fifteen experts on animal husbandry for scientific purposes have pooled their knowledge in a book that is certain to find many users among ecologists as well as others. The sixteen chapters deal with monkey, rat, mouse, guinea pig, hamster, rabbit, dog, cat, ferret, opossum, fowl, reptiles, amphibia, fishes, Drosophila, and laboratory pests and parasites. Invertebrates other than Drosophila are treated only summarily, chiefly as food for fishes, so that the book hardly overlaps the important manual edited by Needham, Galtsoff, Lutz, and Welch, "Culture methods for invertebrate animals" (Ithaca: Comstock Publishing Co. 1937). *E. S. Deevey.*

Gallet, Étienne. 1950. *The flamingos of the Camargue.* 127 pp. Oxford: Basil Blackwell. 15 s. A work of art as much as of natural science, this beautiful book, with its dozens of outstanding photographs, is a poet's account of one of the most remarkable animals left in Europe—*Phoenicopterus ruber roseus* (Pallas). The author, an Arlésien, is a true Provençal, and though years of patient study have gone into the book, technique is never allowed

to obtrude, nor is the recounting of facts permitted to cloud the naturalist's view of the flamingo as an esthetic experience. The facts are of the utmost value none the less. Most interesting is the evidence that this subspecies of flamingo is a mud-eater; there is reason to think that it may be as effective a geologic agent as the prairie dog. *E. S. Deevey.*

Kesteven, G. I. (ed.). 1949. *Malayan fisheries.* viii + 88 pp. Singapore: Malaya Publishing House. $3.50 (Straits). A short but well-rounded account of the fishes and fishing methods of Malaya and Singapore and the importance of fisheries in the human ecology of that region. *J. L. Brooks.*

U. S. Department of Agriculture, Soil Conservation Service. 1950. *Annotated bibliography on sedimentation* (Sedimentation Bulletin No. 2). 351 pp. Washington: Govt. Printing Office. $1.25. A bargain; prepared by a number of U. S. government agencies concerned with problems of sedimentation, under the general direction of L. C. Gottschalk. *E. S. Deevey.*

ANNOUNCEMENTS

Entomological Society of Canada

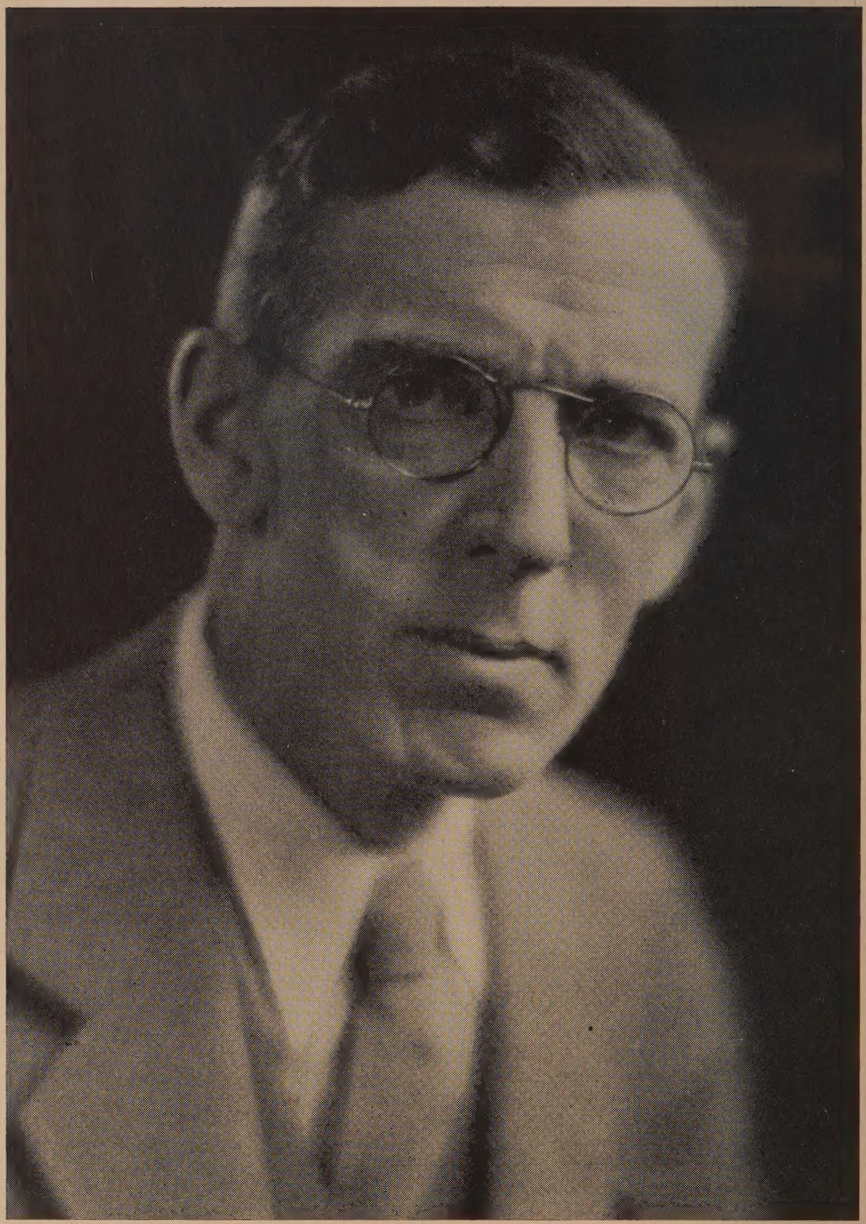
At the eighty-seventh annual meeting of the Entomological Society of Ontario, held at Guelph on November 1–3, 1950, it was decided to form a national society, to be called the Entomological Society of Canada. The new society will serve as a link between the various regional societies, namely, the Acadian Entomological Society, the Entomological Society of Ontario, the Entomological Society of Manitoba, the Entomological Society of British Columbia, the proposed entomological society of Quebec, and others that may be established. *The Canadian Entomologist* will be published jointly by the Ontario and the national societies, Dr. W. R. Thompson continuing as Editor, with Dr. G. C. Ullyett as Associate Editor.

W. A. Ross, Division of Entomology, Ottawa, was elected President and Professor A. W. Baker, Ontario Agricultural College, Guelph, Vice-President. R. H. Wigmore and A. B. Baird, Division of Entomology, Ottawa, have been named Secretary and Treasurer respectively. The Directors comprise the presidents of the regional societies, namely, D. D. Pond, Fredericton, N. B.; W. N. Keenan, Ottawa, Ont.; C. A. Smith, Winnipeg, Man.; and Prof. G. J. Spencer, Vancouver, B. C.; as well as Father O. Fournier, President, Montreal Branch of the Entomological Society of Ontario; Dr. C. W. Farstad, Dominion Entomological Laboratory, Lethbridge, Alta.; and Dr. A. S. West, Queen's University, Kingston, Ont.

The annual meeting of the national society will always be held jointly with the annual meeting of one of the regional societies. In 1951, the combined meetings will be held at Ottawa.

Jackson Hole Research Station

The New York Zoological Society again announces grants-in-aid available for the research program at its Jackson Hole Research Station. The fifth summer program (1951) will include studies in ecology, animal behavior and land management. Further information may be obtained by addressing Director, Jackson Hole Research Station of the New York Zoological Society, Moran, Wyoming.



FORREST SHREVE